



## Full-length Article

## Brain regions associated with moment-to-moment adjustments in control and stable task-set maintenance

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## ABSTRACT

While there is some consensus that cognitive control involves both a capacity to rapidly adjust to unexpected challenges and a capacity to prospectively maintain task-sets over longer timescales, there is disagreement concerning the neural implementation of these capacities. Some accounts, for example, associate rapid adjustments in control with a network of lateral prefrontal and parietal cortices and task-set maintenance with a network of anterior cingulate and insular cortices. Other accounts propose almost the opposite associations. The present study compared these accounts by means of a hybrid fMRI design. Twenty-three right-handed adults were administered a conflict-adaptation paradigm in which the frequency of compatible trials, and therefore, demands on rapid adjustments and stable task-set maintenance, varied parametrically across conditions. Increased demands on moment-to-moment adjustments were associated with a profile of phasic activity in anterior cingulate cortex, anterior insula, and inferior parietal cortex. By contrast, increased demands on stable task-set maintenance were associated with increased sustained activity in medial superior frontal gyrus. Theoretical implications are discussed.

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## Introduction

Cognitive control refers to processes that guide perceptual and motor selection, especially in the face of distraction from irrelevant stimuli or task-inappropriate response tendencies (Miller and Cohen, 2001). Although these processes have a noticeable impact on many everyday behaviors, they are difficult to define in precise terms (Cooper, 2010). According to one recent account (Dosenbach et al., 2008), referred to hereafter as the dual-networks account, the human brain is organized according to the principles of complex systems (Sporns, 2010), with an architecture reminiscent of small-world networks and multiple complementary controllers. These controllers include a cingulo-opercular (or CO) network, comprised of dorsal anterior cingulate and anterior insular cortices, and a fronto-parietal (or FP) network, comprised of densely interconnected lateral prefrontal and superior parietal cortices. CO and FP networks are viewed as complementary insofar as they operate over different timescales, with the FP network supporting moment-to-moment adjustments in control over short timescales, and the CO network supporting stable task-set maintenance over longer timescales.

The dual-networks account provides both a novel approach to the conceptualization of cognitive control, especially through its use of

graph theory and associated metrics, and an extension of earlier suggestions that cognitive control be viewed as an emergent product of multiple interacting processes each associated with distinct networks within prefrontal, cingulate, and parietal cortices. Seeley et al. (2007), for example, suggest two networks underlie cognitive control: a “salience network” comprising dorsal anterior cingulate (dACC) and anterior insular (AI) cortices, and an “executive control” network comprising dorsolateral frontal and superior parietal cortices (Seeley et al., 2007). Similarly, Botvinick and colleagues distinguish dACC-mediated monitoring processes that signal the need for control and lateral PFC-mediated executive processes that resolve perceptual and motor conflicts (Botvinick et al., 2001). Finally, Braver and colleagues have proposed dual proactive and reactive mechanisms underlying cognitive control, with proactive control serving as a source of top-down future-oriented bias that can facilitate processing of upcoming events, and reactive control serving as a late correction mechanism that is mobilized only as needed. These mechanisms are thought to be associated with distinct profiles of activation in PFC, with proactive control associated with sustained activation in lateral PFC and reactive control associated with transient signals in lateral prefrontal and dorsal anterior cingulate cortices (Braver et al., 2007).

Closer examination, however, reveals several points of contrast between these accounts. One concerns functional characterizations of anterior cingulate and insular cortices. According to the dual-networks account (Dosenbach et al., 2008), these regions support the stable maintenance of task-sets over extended time periods. This contrasts with other accounts that maintain anterior cingulate (Botvinick et al., 2001; Ridderinkhof et al., 2004; Seeley et al., 2007)

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and insular cortices (Menon and Uddin, 2010; Seeley et al., 2007) are intimately involved in rapid on-line adjustments in control. According to Menon and Uddin (2010) for example, the AI and dACC are core members of a larger salience network that rapidly activates to stimuli of potential motivational relevance, such as stimuli that are temporally or spatially infrequent. These transient signals help direct attention to the external environment by activating and disengaging executive and default-mode networks respectively (for discussion, see Menon and Uddin, 2010). Similarly, Botvinick et al. (2001) argue that the dACC rapidly signals the need for top-down control in the face of transient conflicts between competing response pathways. Consistent with this idea, transient activity in dACC varies with parametric manipulations in response conflict (Durston et al., 2003; Forster et al., 2010) and predicts DLPFC activity (Kerns et al., 2004; Liston et al., 2006) and the magnitude of behavioral adjustment (Forster et al., 2010) on subsequent trials. A second point of contrast concerns the functional characterization of lateral prefrontal and parietal cortices. The dual-networks account argues that fronto-parietal cortices support moment-to-moment adjustments of control, such as initiations of attention and responses to feedback that occur quickly on relatively short timescales. This contrasts with idea that lateral prefrontal cortex, and dorsal regions in particular, support the active maintenance of task-relevant information (Miller and Cohen, 2001), such as attention-guiding rules (MacDonald et al., 2000) by means of protracted periods of sustained activity (Funahashi et al., 1993; Fuster et al., 2000).

Despite a very rich literature documenting the neural correlates of cognitive control, there are relatively few studies that permit a direct comparison of these alternative accounts. The primary constraint is that most studies have utilized standard event-related fMRI designs that are well-suited to detecting phasic signal changes associated with relatively short-lived processes, such as moment-to-moment control adjustments, but not well-suited to detecting tonic signal changes associated with processes that span longer timescales, such as task-set maintenance. Hybrid designs, in which individual trials are jittered in their presentation timing to permit event-related analysis, but also grouped into multi-trial conditions to permit block-level analysis (Visscher et al., 2003), are an attractive alternative as they allow the modeling of both phasic (event-related) and tonic (block-level) signal changes, and therefore the possibility of identifying and comparing the neural correlates of moment-to-moment control and stable task-set maintenance (Dosenbach et al., 2008).

Therefore, in the present study, we parametrically varied demands on moment-to-moment control and task-set maintenance through the use of a conflict adaptation paradigm, and administered the paradigm in the form of a hybrid design so that phasic and tonic signal changes associated with these manipulations could be modeled simultaneously. Individual trials of a standard size-congruency task (Banks and Flora, 1977; Henik and Tzelgov, 1982) were presented with a jittered inter-trial interval and in blocks that differed in the frequency of compatible trials (75%, 50%, and 25%). On each trial, participants were presented two digits that differed in numerical magnitude and physical size, and indicated by means of a button press which was numerically larger. As responses based on differences in physical size are typically faster than responses based on differences in numerical magnitude, responses to incompatible stimuli (i.e., pairs in which the numerically larger digit was physically smaller) are typically slower and more error-prone than responses to compatible stimuli (i.e., pairs in which the numerically larger number is physically larger), a phenomenon referred to as the size congruity effect, or SCE (Banks and Flora, 1977; Henik and Tzelgov, 1982). The magnitude of the SCE adapts to changes in the condition-level frequency of compatible trials, being largest, intermediate, and smallest in 75%, 50%, and 25% compatible conditions respectively (Borgmann et al., 2011). The advantage over other stimulus-response compatibility tasks such as the color-word Stroop task is that there

are many variants of compatible and incompatible stimuli in the size congruency task. Consequently, stimulus repetitions, which are an important confound in studies of conflict adaptation (Mayr et al., 2003), can be easily eliminated from the design.

We reasoned that varying the frequency of compatible trials within conditions introduces parametrically varying demands on task-set maintenance and moment-to-moment control. Specifically, we reasoned that when compatible trials are infrequent, participants establish a task set for ignoring physical size and focusing on magnitude comparison, which, in turn, diminishes the need to adjust in the moment to any individual incompatible stimulus. However, as compatible trials become more frequent in a condition, participants increasingly rely on congruent physical size cues as a basis for their responses, which in turn increases the need to adjust in the moment to any individual incompatible stimulus. Therefore, we reasoned that a search for voxels in which event-related responses to incompatible and compatible stimuli scale parametrically with changes in the block-level frequency of compatible trials would reveal brain regions associated with the implementation of moment-to-moment adjustments in control. By contrast, a search for voxels in which block-level activity parametrically increases with parametric decreases in the block-level frequency of compatible trials would reveal regions associated with stable task-set maintenance (see Fig. 1).

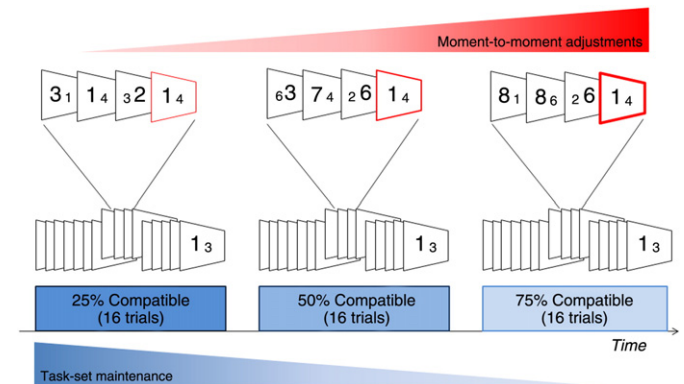
## Methods

### Participants

Participants included 26 right-handed young adults (12 male) who ranged in age from 21 to 35 years. All participants had normal or corrected-to-normal vision, and reported no history of neurological or psychiatric illness. Data from three participants were excluded from the analysis, one due to equipment malfunction and two due to excessive motion. Participants provided written consent to their participation prior to data collection. All aspects of the study were conducted in accordance with the Declaration of Helsinki.

### Task

Participants were administered a size congruency task, in which on each trial, two white digits differing both in physical and numerical magnitude were presented simultaneously on a black background



**Fig. 1.** An illustration of the experimental paradigm. Two digits that differed in physical and numerical magnitude were presented on each trial, and participants selected the numerically larger digit by means of a button-press. On compatible trials, the numerically larger digit was physically larger; on incompatible trials, the numerically larger digit was physically smaller. Individual trials were administered with a jittered ITI in 16-trial blocks that varied in terms of the proportion of compatible trials within the condition. Demands on moment-to-moment adjustment parametrically increased with increases in the block-level proportion of compatible trials; demands on task-set maintenance increased with decreases in the block-level proportion of compatible trials.

for 950 ms (see Fig. 1). Digits included numbers 1 through 9; physically large digits appeared in 60 point font; physically small digits appeared in 30 point font. On compatible trials, the numerically larger digit was physically larger. On incompatible trials, the numerically larger digit was physically smaller. Participants selected the numerically larger of the two digits by depressing a key that corresponded with the location of the numerically larger digit (i.e., left or right) using their right hand. The response deadline was equal to the stimulus duration (950 ms) and no feedback was provided. Individual trials were grouped into 16-trial blocks that differed in terms of the proportion of trials in the block that were compatible. Thus, in High-Frequency blocks, 75% of trials (or 12 of 16) were compatible; in Medium-Frequency blocks, 50% of trials (or 8 of 16) were compatible; and in Low-Frequency blocks, 25% of trials (or 4 of 16) were compatible. An additional three anchor trials were added to the beginning of each block as a means of establishing expectations about the frequency of compatible trials within the block, but were modeled separately using a predictor of no interest. For High-Frequency blocks, all three anchor trials were compatible; for Medium-Frequency blocks, either one or two trials were compatible, and for Low-Frequency blocks, none were compatible. Trials within blocks were presented in a random order that was fixed for all participants, and were randomly jittered by means of an inter-trial interval (or ITI) that ranged from 2500 ms to 5500 ms ( $M = 4000$  ms) in 500 ms increments. Blocks were presented in a random order fixed for all participants and were separated by 10-second intervals. During all inter-trial and inter-block intervals, participants remained fixated on a centrally-presented white cross. In total, individual participants completed 24 separate blocks of trials (8 each of High-, Medium-, and Low-Frequency) for a total of 384 individual trials. The entire task was administered in two separate 18-minute runs.

#### *MRI data acquisition*

MRI data were collected using a 3 T Siemens TimTrio MRI scanner fitted with a Siemens 32-channel head coil (Siemens Medical Solutions, Erlangen, Germany). Functional volumes consisted of 36 slices acquired parallel to the ACPC axis using an interleaved slice acquisition order and an echo-planar imaging pulse sequence (TR = 2000 ms, TE = 30 ms, flip angle =  $78^\circ$ ,  $64 \times 64$  matrix,  $21.1 \times 21.1$  cm FOV,  $3 \times 3 \times 3$  mm voxel resolution). A total of 1486 functional volumes were collected from each participant over two separate 743-volume runs. In addition, a high-resolution anatomical scan (192 slices,  $256 \times 256$  matrix,  $21.1 \times 21.1$  cm FOV,  $1 \times 1 \times 1$  mm voxel resolution) was acquired from each participant to assist in visualizing the results of functional analyses.

#### *fMRI data preprocessing*

Data were preprocessed using BrainVoyager QX (Brain Innovation BV, Maastricht, Netherlands). Prior to preprocessing, motion parameters were calculated for each run. Motion was constrained to 2.0 mm within runs, leading to the removal of three runs from the data.

Data were subsequently motion-corrected by aligning each functional volume with the first volume of the first run, within subjects. Linear trend removal was applied to the timecourses of motion-corrected functional runs. T1-weighted anatomical scans were aligned to ACPC axis, and normalized to Talairach and Tournoux (1998) stereotactic space. T2\*-weighted functional volumes were then automatically aligned to unwarped anatomical images by means of a gradient-based affine alignment algorithm. Functional volumes were then warped into Talairach space by applying the translation and rotation parameters used to warp the anatomical images into Talairach space. Functional

volumes were then smoothed using an 8 mm full-width at half maximum Gaussian kernel.

#### *Statistical analysis*

Data were analyzed using BrainVoyager QX (Brain Innovation BV, Maastricht, Netherlands). Phasic and sustained BOLD responses were simultaneously estimated by means of a whole-brain mixed RFX General Linear Model (GLM) that included event- and block-level predictors described below. Contrasts of event- and block-level parameter estimates generated by the model were then conducted as a means of identifying voxels associated with moment-to-moment adjustments in control and stable task-set maintenance respectively.

#### *Identifying voxels involved in moment-to-moment adjustments in control*

By design, demands on moment-to-moment adjustments in control increased with parametric increases in the frequency of compatible trials within conditions (see Fig. 1). Of interest then were voxels in which: (1) event-related responses to incompatible trials parametrically increased as the frequency of compatible trials within a condition parametrically increased; and (2) event-related responses to compatible trials parametrically decreased as the frequency of compatible trials within a condition parametrically increased. These voxels were identified by estimating the difference in the beta coefficients of two scaled event-related predictors included in a whole-brain mixed RFX GLM, one for incompatible and one for compatible trials. The scaled predictor for incompatible trials was formed by: (1) defining a vector of onsets for all correct incompatible trials in a run (not including anchor trials, which were assigned to a predictor of no interest) and then using this to create a standard event-related stick-function for all incompatible trials; (2) scaling individual instances (i.e., the height of individual sticks) according to the frequency condition in which they occurred, such that individual incompatible trials in the 75%, 50%, and 25% conditions were scaled 0.75, 0.50, and 0.25 respectively; and (3) convolving the resulting stick-function with a canonical sum of two gammas hemodynamic response function. The scaled predictor for the compatible trials was formed the same way except that the initial vector of onsets included all correct compatible trials in the run (not including anchor trials, which were assigned to a predictor of no interest). In the context of a GLM, the beta coefficients of these predictors will be positive when the magnitude of BOLD response increases with condition-level increases in the frequency of compatible trials, and negative when the magnitude of the BOLD response decreases with condition-level increases in the frequency of compatible trials. Therefore, to identify regions associated with moment-to-moment adjustments in control, we included these two scaled predictors in a whole-brain RFX mixed GLM (described above), and mapped the difference in the beta coefficients of these two scaled predictors (i.e.,  $\beta_{\text{Scaled INC}} - \beta_{\text{Scaled CON}}$ ), correcting for multiple comparisons at  $q$  (FDR)  $< .05$ . To visually confirm that these regions showed the specific interaction of Condition and Trial Type that was of interest, we ran a whole-brain RFX mixed GLM with six separate predictors for all levels of Condition and Compatibility, two predictors for trials of no interest (i.e., errors and anchor trials) and three block predictors (one for each condition). We then extracted and plotted the six (i.e.,  $3 \text{ Condition} \times 2 \text{ Compatibility}$ ) beta coefficients from regions in which the difference in the scaled predictors was supra-threshold.

#### *Identifying voxels involved in stable task set maintenance*

By design, demands on stable task-set maintenance increased with block-level decreases in the frequency of compatible trials.

Of interest then were voxels that showed sustained block-level responses that increased with parametric decreases in the block-level frequency of compatible trials. To identify these voxels, onset and offset times for each of the three 16-trial conditions were used to create three separate boxcar functions, one for each condition. These boxcar functions were then convolved with a standard sum of two gammas hemodynamic response function and were included as predictors in a whole-brain RFX mixed GLM (described above). A one-factor Analysis of Variance (ANOVA) of the beta coefficients of these three predictors revealed voxels that showed a significant difference in sustained activity across conditions, with the resulting map corrected for multiple comparisons at  $q$  (FDR) < .05. Beta coefficients were then extracted from these regions for the purpose of visualizing the nature of the condition effect.

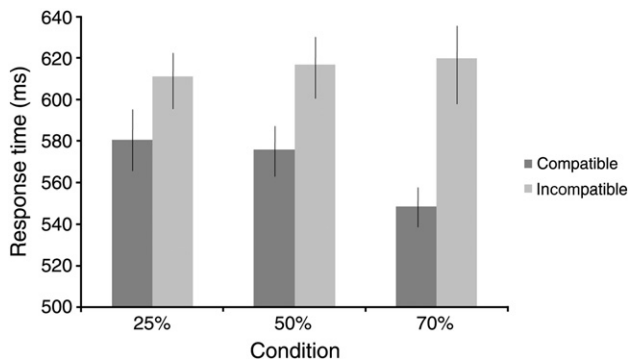
### Region of interest analyses

It is possible that regions found to be associated with moment-to-moment adjustments in control might also show sustained BOLD responses reflective of involvement in stable task-set maintenance. To test this, we extracted beta coefficients of the three block predictors from several of these regions and tested, by means of a one-way repeated-measures ANOVA, whether these regions exhibited sustained signals indicative of involvement in stable task-set maintenance.

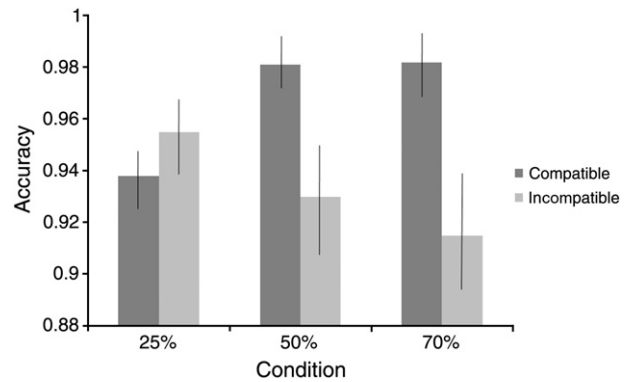
## Results

### Behavioral data

Response time and accuracy are plotted in Figs. 2 and 3. A 3 Condition  $\times$  2 Compatibility repeated-measures ANOVA confirmed an effect of Compatibility on response time,  $F(1, 22) = 80.3$ ,  $p < .05$ , and accuracy,  $F(1, 22) = 13.7$ ,  $p < .05$ , such that responses to incompatible stimuli were slower and more error-prone than responses to compatible trials. There was also an effect of Condition on response time,  $F(2, 44) = 4.0$ ,  $p < .05$ , such that responses were slower in the 25% (mean RT = 596 ms) and 50% (mean RT = 596 ms) compared with the 75% (mean RT = 585 ms) conditions. Finally, there was a significant interaction of Condition and Compatibility on response time,  $F(2, 44) = 16.4$ ,  $p < .05$ , and accuracy,  $F(2, 44) = 12.6$ ,  $p < .05$ . Post-hoc tests (Bonferroni-corrected for multiple comparisons) confirmed that the effect of Condition differed for compatible and incompatible stimuli. For compatible stimuli, responses were faster in the 75% as compared to the 50% and 25% conditions, and more accurate in the 75% and 50% as compared to the 25% conditions. For incompatible stimuli by contrast, responses were more accurate in the 25% than in the 75% condition.



**Fig. 2.** Response times plotted as a function of Condition (i.e., 25%, 50%, or 75% compatible) and Compatibility (i.e., Compatible and Incompatible). Error bars show one SE above and below the mean.



**Fig. 3.** Behavioral accuracy as a function of Condition (i.e., 25%, 50%, or 75% compatible) and Compatibility (i.e., Compatible and Incompatible). Error bars show one SE above and below the mean.

To guard against the possibility that the pseudo-randomized block order administered to all participants may have unduly influenced performance, we tested for differences in behavioral performance between blocks administered early and those administered late in the testing session. A 2 Order (early, late)  $\times$  3 Condition (25%, 50%, 75%)  $\times$  2 Compatibility (compatible, incompatible) repeated-measures ANOVA on response time revealed effects of Compatibility,  $F(1, 19) = 25.9$ ,  $p < .01$ , and Condition,  $F(2, 38) = 6.5$ ,  $p < .01$ , and an interaction of Compatibility and Condition,  $F(2, 38) = 12.1$ ,  $p < .01$ , but no effects of Order and no higher-order interactions involving Order. An identical analysis on accuracy revealed an effect of Compatibility, but no effects or interactions involving Order.

### fMRI data

#### Moment-to-moment adjustments in control

Brain regions associated with moment-to-moment adjustments in control are displayed in Fig. 4 and listed in Table 1, and included anterior insula bilaterally, right anterior cingulate cortex, dorsolateral prefrontal cortex bilaterally, and right inferior parietal cortex. Visual inspection of the beta coefficients extracted from these regions confirmed that the event-related BOLD response in these regions: (1) was greater for incompatible than for compatible trials; and (2) decreased for incompatible trials and increased for compatible trials as the condition-level frequency of compatible trials decreased.

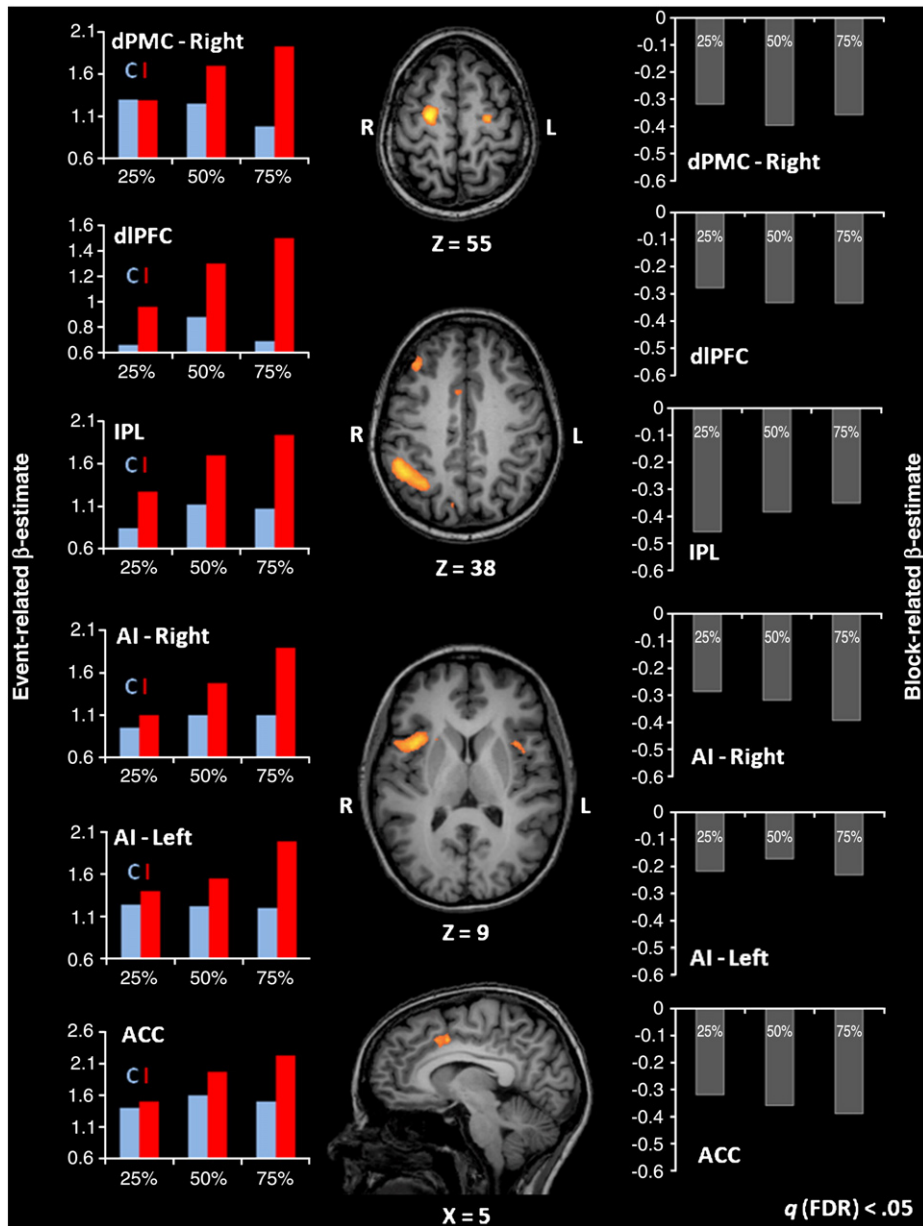
#### Stable task-set maintenance

Brain regions associated with stable task-set maintenance are displayed in Fig. 5 and listed in Table 1, and consisted primarily of a cluster of voxels along the medial surface of the superior frontal gyrus. Visual inspection of the beta coefficients extracted from this region confirmed that a linear increase in sustained activity in this region was associated with a decrease in the condition-level frequency of compatible trials.

### ROI analyses

Region of interest analysis examined whether regions associated with moment-to-moment adjustments in control also showed sustained BOLD activity that increased in association with changing demands on task-set maintenance. Beta coefficients of the three block predictors are presented for four such regions, including anterior insula, anterior cingulate cortex, dorsolateral prefrontal cortex, and inferior parietal cortex (see Fig. 4). There was no evidence that increased demands on stable task set maintenance was associated with increased sustained BOLD activity in these any of these regions.





**Fig. 4.** Brain regions associated with moment-to-moment adjustments in control. dPMC = dorsal premotor cortex; dIPFC = dorsolateral prefrontal cortex; IPL = inferior parietal lobule; AI = anterior insula; ACC = anterior cingulate cortex. All images are corrected for multiple comparisons,  $q(FDR) < .05$ . Beta estimates on the left were computed from event-related predictors, with estimates for compatible and incompatible trials in blue and red respectively. Beta estimates on the right were computed from block predictors. Individual estimates are based on an average of all voxels in each cluster, and are presented without error bars as they were extracted only for the purpose of visualization.

## Discussion

According to the dual-networks account, moment-to-moment adjustments in control and stable task-set maintenance are separate control processes that involve distinct networks operating on different timescales. The goal of the present study was to investigate these ideas through the use of fMRI. Participants were administered a size-congruency task in which individual trials were grouped into separate conditions that differed in terms of the frequency of compatible trials within the condition (i.e., 25%, 50%, and 75%). As expected (Borgmann et al., 2011), behavioral interference effects increased with parametric increases in the frequency of compatible trials within a condition. These adaptation effects were not attributable to either stimulus or response repetition effects (Mayr et al., 2003) as there were no stimulus repetitions in this paradigm, and given randomization of the stimulus sequence, the probability of response repetition for both compatible and incompatible trials

was close to .5. In our view, these effects reflect complementary changes in the demands on stable task-set maintenance and moment-to-moment adjustments in control across conditions. In the 25% condition, participants faced repeated instances of response conflict, and in response, prospectively prepared for future instances of conflict through a sustained focus on magnitude comparison. This was reflected by the fact that in the 25% condition: (a) responses to incompatible stimuli were comparatively fast, suggesting participants were less distracted by incongruent physical size cues; (b) responses to compatible stimuli were comparatively slow, suggesting participants were focused on magnitude comparison, and therefore missed the opportunity to benefit from congruent physical size cues. Given that participants were prepared in advance for conflict under these conditions, demands on moment-to-moment adjustments were relatively low. By contrast, in the 75% condition, sustaining a focus on magnitude comparison was unnecessary, as participants took advantage of congruent size cues when formulating responses (as

**Table 1**

Summary of regions associated with moment-to-moment adjustments in control and stable task-set maintenance.

Region	BA	Hemisphere	X	Y	Z	Cluster size	Peak voxel statistic
<i>Moment-to-moment adjustments</i>							
ACC	24	R	5	11	42	416	$t(22) = 5.29$
AI	13	L	-35	12	10	31	$t(22) = 4.47$
		R	40	16	5	2727	$t(22) = 6.09$
dlPFC	9/46	R	35	46	20	355	$t(22) = 4.77$
		R	39	33	39	233	$t(22) = 5.32$
		L	-32	38	28	129	$t(22) = 4.85$
dPMC	6	L	-23	-10	51	768	$t(22) = 7.31$
		R	23	-7	55	1706	$t(22) = 6.28$
IFJ	6/8	R	41	2	32	206	$t(22) = 4.55$
IPC	40	R	45	-49	32	6674	$t(22) = 6.07$
<i>Stable task-set maintenance</i>							
Medial SFG	9	L	-5	36	39	697	$F(2, 44) = 23.1$
Fusiform gyrus	37	R	34	-68	-12	1170	$F(2, 44) = 18.5$

X, Y, and Z are the Talairach coordinates of the peak voxel in each region. ACC = anterior cingulate cortex; AI = anterior insula; dlPFC = dorsolateral prefrontal cortex; dPMC = dorsal premotor cortex; IFJ = inferior frontal junction; IPC = inferior parietal cortex; SFG = superior frontal gyrus. Cluster size is measured in mm<sup>3</sup>.

reflected in comparatively faster responses to compatible stimuli). This however left them relatively unprepared to manage particular instances of conflict (as reflected by comparatively slower responses to incompatible stimuli). Given that participants were less prepared for conflict under these conditions, rapid on-line adjustments in control were required to ensure accurate performance.

Analyses of fMRI data revealed several sets of findings concerning the neural correlates of moment-to-moment adjustments in control and stable task-set maintenance, which will be discussed in turn.

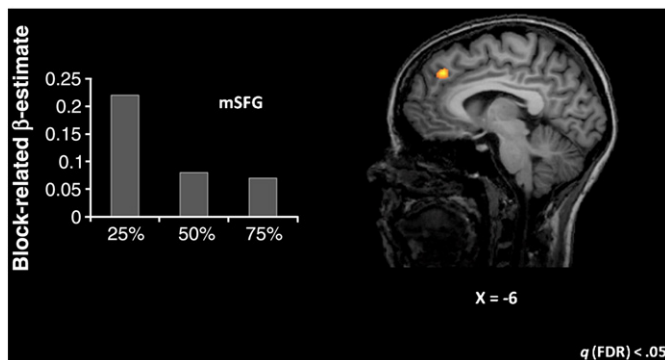
#### *Moment-to-moment adjustments in control*

Estimates of phasic BOLD responses identified several regions associated with the implementation of moment-to-moment adjustments in control, including the anterior cingulate cortex, the anterior insula, dorsolateral prefrontal cortex, and inferior parietal cortex. These regions responded more strongly to incompatible stimuli and more weakly to compatible stimuli as the frequency of compatible trials within conditions (and by extension, the need for rapid adjustments in control) increased. Moreover, targeted ROI analyses in these regions found no evidence of changes in sustained activity

with increased demands on task-set maintenance. These findings are consistent with a number of studies that report functional activation in these regions. Activity in the anterior cingulate cortex, for example, has been associated with a variety of processes that initiate rapid adjustments in behavior (for review, see Ridderinkhof et al., 2004), including error-processing (Debener et al., 2005), conflict monitoring (Botvinick et al., 2001; Liston et al., 2006; MacDonald et al., 2000) and dynamic coding of action values (Behrens et al., 2007; Holroyd and Coles, 2002; Jocham et al., 2009) and also predicts future adjustments in control, with more robust response to conflict predicting greater attenuation of behavioral interference in subsequent trials (Kerns et al., 2004; Liston et al., 2006). The anterior insula (AI) has traditionally been viewed as part of the limbic system, and much of the critical thinking concerning its function has focused on its role in interoception (Craig, 2003; Critchley et al., 2004) and socio-emotional processing/awareness (Baumgartner et al., 2009; Craig, 2010; Singer et al., 2009). However, more recently, the AI has been linked to dynamic adjustments in higher-order control processes (for review, see Menon and Uddin, 2010). The AI co-activates with the ACC in response to errors (Klein et al., 2007), response inhibition (Barber and Carter, 2005), task switching (Cole and Schneider, 2007), and interference suppression (Bunge et al., 2002; Levens and Phelps, 2010), and there is some evidence that the AI functions like a hub, engaging and disengaging large-scale brain networks to meet changing information processing demands (Sridharan et al., 2008).

Moment-to-moment adjustments in control were also associated with activity in the inferior parietal cortex. Parietal cortex activation occurs in response to a variety of cognitive control demands including conflict processing (Liston et al., 2006), attention and response switching (Barber and Carter, 2005; Crone et al., 2006; Morton et al., 2009; Rushworth et al., 2001) and active maintenance of information of working memory (Olesen et al., 2004) and is commonly observed in the context of larger cognitive control (Cole and Schneider, 2007; Duncan, 2010) or attention (Corbetta and Shulman, 2002) networks.

In the present experiment, ACC, AI, dorsolateral prefrontal and inferior parietal cortices responded more strongly to incompatible stimuli and more weakly to compatible stimuli as the frequency of compatible trials within conditions increased, which is consistent with the idea that these regions support rapid moment-to-moment adjustments in control. There are, however, several interpretations of what these adjustments might consist of. One possibility is that this profile of activation reflects conflict monitoring, such that activity in these regions increases with increases in conflict between incompatible responses (but see Liston et al., 2006). With respect to incompatible stimuli, conflict of this kind is likely to increase as the frequency of compatible trials increases given less advanced preparation for conflict under these circumstances (Kerns et al., 2004; Botvinick et al., 2001; Forster et al., 2010). And although compatible stimuli are not typically associated with response conflict, it is possible that when compatible stimuli are very frequent, they are less likely to be associated with the simultaneous activity of two incompatible responses as participants take fuller advantage of the irrelevant but compatible feature of the stimulus under these circumstances. An alternate but related possibility is that this profile of activation reflects behavioral uncertainty, with greater activation occurring in association with greater uncertainty about which of available responses to enact (Singer et al., 2009). This uncertainty would presumably be greater for incompatible than compatible stimuli, but would also increase as stimuli (either compatible or incompatible) become increasingly unexpected. Thus, activation would be greater to unexpected (i.e., infrequent) than expected (i.e., frequent) incompatible stimuli, but would also be greater to unexpected (i.e., infrequent) than expected (i.e., frequent) compatible stimuli. Thus, the AI, ACC, dlPFC and IPL may play an integral role



**Fig. 5.** Brain regions associated with task-set maintenance. mSFG = medial superior frontal gyrus. The image was corrected for multiple comparisons,  $q$  (FDR) < .05. Beta estimates are based on an average of all voxels in the cluster, and are presented without error bars as they were extracted only for the purpose of visualization.

in moment-to-moment adjustments in control insofar as these regions signal instances of behavioral uncertainty. Still, whatever the precise nature of the underlying processing may be, the findings implicate AI, ACC, dlPFC and parietal cortex in moment-to-moment adjustments in control.

#### *Stable task-set maintenance*

Estimates of sustained BOLD responses identified a region on the medial surface of the superior frontal gyrus. This region showed a sustained response that strengthened as the block-level frequency of compatible trials decreased (and by extension, demands on stable task-set maintenance increased). These findings parallel those of Ansari and colleagues who found activity in this region associated with stimulus–response incompatibility in a size congruency task (Ansari et al., 2006). These findings also parallel the results of Summerfield and colleagues who examined the neural correlates of perceptual set in the context of an object identification task (Summerfield et al., 2006). As in the present study, they found a region in dorsal medial prefrontal cortex that showed a sustained signal associated with the maintenance of a mental set, although their findings concern the maintenance of a perceptual set related specifically to face processing. Whatever mental set participants maintained in the present study, it likely related more to a particular type of processing (e.g., magnitude comparison), than a particular class of stimuli. In any case, these findings are at least suggestive, and point to a possible role for dorsal regions of medial prefrontal cortex in maintaining task sets.

#### *Implications for models of cognitive control*

The current findings have implications for several models of cognitive control. According to the dual-networks account, for example, cognitive control is not monolithic, but is comprised of distinct moment-to-moment adjustment and task-set maintenance processes. Moment-to-moment adjustment occurs over relatively short timeframes, and is implemented by a putative fronto-parietal network comprised of the dorsal attentional network (Corbetta and Shulman, 2002) as well as lateral prefrontal and inferior parietal cortices. Stable task-set maintenance on the other hand operates over an entire task epoch, as when task-related information is integrated over numerous trials, and is supported by a putative cingulo-opercular network comprised of the ACC, the AI, and the frontal operculum. The current findings offer some support for the dual-networks account. For example, we found event- and block-related signals associated with transient and stable demands on control respectively, consistent with suggestion from the dual-networks account that cognitive control comprises multiple processes that operate on different timescales. As well, we found that moment-to-moment adjustments were associated with activity in inferior parietal cortex and lateral prefrontal cortex, as predicted by the dual-networks account.

There were however, several findings that were inconsistent with the dual-networks model. In particular, there was no evidence of an association between ACC and the AI and stable task-set maintenance. On the contrary, these regions were strongly associated with moment-to-moment adjustments in control. In our view, these findings are more easily accommodated by other models of cognitive control including the salience network model of ACC and AI function (Menon and Uddin, 2010; Seeley et al., 2007), the conflict-monitoring model (Botvinick et al., 2001), and the dual mechanisms of control account (Braver et al., 2007). According to the salience network model, the ACC and AI support bottom-up salience processing by tagging infrequent but relevant stimuli as salient. Having highlighted behaviorally-relevant stimuli in this way, the salience network garners the necessary resources to ensure such stimuli are adequately processed by engaging executive and disengaging default mode

networks respectively. The conflict-monitoring model, while directed more at characterizing the function of the ACC, suggests dorsal cingulate cortex monitors for response conflict, and signals lateral prefrontal cortex of the need for top-down control. Finally, the dual mechanisms of control theory propose distinct proactive and reactive control mechanisms. On this account, reactive control, supported in part by the ACC, is a late-correction mechanism that can be rapidly engaged in the face of behaviorally-relevant but unanticipated demands. Despite their differences, these models share the view that the AI and, in particular, the ACC respond rapidly to salient or unexpected events and dynamically adjust top-down control settings by signaling other executive control areas. As such, these models are well-positioned to accommodate the findings of the current study.

#### *Strengths, weaknesses, and future directions*

There are several important strengths to the current study, including the use of a hybrid or mixed fMRI design (Visscher et al., 2003), and the parametric manipulation of demands on moment-to-moment adjustment and stable task-set maintenance. By implementing both design considerations, we were able to examine both trial-to-trial and sustained signals (for discussion of the merits of hybrid designs in studies of cognitive control, see Dosenbach et al., 2008), and to test for particular patterns of responses to our experimental manipulations (for discussion of the merits of parametric designs, see (Braver et al., 1997)).

While suggestive, the current results are based on particular operational definitions of moment-to-moment adjustments and stable task-set maintenance that may depart from the spirit of the ideas laid out in the dual-networks model. Indeed, in distinguishing these processes, Dosenbach and colleagues emphasize differences in the way these processes utilize start-cues and performance feedback, as well as difference in their relative accessibility. While in our opinion, use of a conflict adaptation paradigm was a valid means of probing moment-to-moment adjustments and stable task-set maintenance, our paradigm was devoid of explicit cues and performance feedback. Whether a different choice of operational definitions would significantly alter the mapping of these respective networks remains an important question for future research.

Finally, whereas in the dual-networks account, networks are conceptualized using sophisticated multivariate techniques, the current results are based on standard voxel-wise univariate statistics. As such, it is unclear to what extent the current findings reflect the existence of bona fide networks. An important challenge for future research then would be to examine the structure and activity time-courses of underlying networks associated with conflict adaptation, as is possible, for example, with blind-source separation techniques such as ICA (Calhoun et al., 2009).

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