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Cognitive control: Preparation of task switching components

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ABSTRACT

Task performance often improves when tasks can be prepared in advance. However, the mechanisms that support advance preparation are highly debated. Proceeding under the hypothesis that switch-specific neural activation during advance preparation is the hallmark of controlled processing, this study investigates the behavioral and neural effects of component preparation during task-switching. Toward this end, fMRI was used to observe neural activity during preparation of response rules (RULE task) compared to preparation of stimulus set (PERCEPTUAL task). We predicted that switch-specific activation would be observed for RULE and PERCEPTUAL switching when component preparation was isolated from target-related activation. The results indicated that preparation for both tasks was supported by common regions of activation; however preparation for switches of response rule was supported by switch-specific activation of the anterior cingulate (ACC) and left lateral prefrontal cortex (LPFC). Shift-cost was also eradicated in this condition with enough preparation time, and was associated with an increase in ACC activation. Switches of stimulus set were not marked by specific neural activity during the preparation interval. While the amount of preparation time affected overall performance, PERCEPTUAL task switches did not benefit more from preparation time than task repeats. It was concluded that response rules can be reconfigured pre-target due to the support of ACC-LPFC activation, where preparation of stimulus sets is supported by a general type of configuration common to both components.

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1. Introduction

Cognitive control is a biasing mechanism which determines whether information gains access to or output from the cognitive system (Botvinick et al., 2004; Meiran et al., 2008; Miller and Cohen, 2001). Task switching is argued to be a marker of cognitive control because of the need to bias task-relevant information when frequently switching between tasks (Rogers and Monsell, 1995, although see Allport, Styles, and Hsieh, 1994). Demand during task switching is measured in terms of shiftcost, the disparity in response time between trials in which a task has switched and trials in which a task is repeated. The strongest support for the involvement of cognitive control in task switching has been the reliable observation of the *prepara*tion *effect* (Kiesel et al., 2010; Meiran, 2000; Monsell, 2003). When manipulated within-subjects (Altmann, 2004), increase in preparation time has been empirically demonstrated to reduce shiftcost (Kiesel et al., 2010; Meiran, 2000; Monsell, 2003). However, contention has emerged over the mechanisms that drive the preparation effect; for example, whether control is specific to a particular task component (e.g., rule loading, attentional selection; Bunge et al., 2003; Chiu and Yantis, 2009; Esterman et al., 2009; Kim et al., 2011, 2012; Ravizza and Carter, 2008; Rushworth et al., 2002; Wager et al., 2005). The goal of the

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current study is to assess the action of preparatory control in task switching with fMRI by characterizing neural activation during component preparation.

Proponents of the controlled processing account of preparation argue that shift-cost is reduced with preparation due to pre-target reconfiguration (i.e. 'mental-gear changing,' in Monsell, 2003). This position has been handled formally by assuming the presence of control modules, for example changedetection (Brown et al., 2007) or input-biasing modules (Meiran et al., 2008), or controlled processing stages (e.g., Prepareswitch production, Sohn and Anderson, 2001) that act primarily on switch trials. Opponents of the switch-specific configuration account argue that shift-cost is an emergent property of a general configuration process that occurs on both repeat and shift trials (Altmann, 2003, 2004; Altmann and Gray, 2008; Logan and Bundesen, 2003, 2004). For example, Altmann and Gray (2008) propose that a type of semantic retrieval occurs on every trial, which is faster for repeat than switch trials due to the priming of relevant task representations. Thus, a shift-cost emerges as a function of the disparity in retrieval priming, which is absorbed by an increase in preparation time (Altmann and Gray, 2008).

The distinction between the switch-specific configuration and general configuration frameworks lies in the nature of configuration that occurs during preparation for repeat and switch trials. The former account suggests that the system benefits from a pre-target *reconfiguration* mechanism more or less *specific* to switch trials, whereas the latter proposes a general type of configuration that occurs on every trial regardless of trial-type (i.e. repeat or switch). Competing computational models have demonstrated that both theoretical frameworks can adequately account for the preparation effect (Altmann and Gray, 2008; Brown et al., 2007; Gilbert and Shallice, 2002; Logan and Bundesen, 2003; Meiran et al., 2008; Sohn and Anderson, 2001; Yeung et al., 2006), leaving the debate in search of a convergence of support from alternative methodologies.

Neuroimaging techniques, including EEG and fMRI, have offered a promising avenue to help resolve the debate by affording the ability to observe and dissociate the action of the putative underlying control mechanisms. This research has proceeded under the hypothesis that if task switching is special (i.e. a controlled process) then neural activity should be increased for switch trial preparation compared to repeat trials. Additionally, switching efficiency should be systematically associated with the amplitude of neural activity; that is, greater activity should be observed when switching is more efficient.

Initial evidence from EEG studies on advance preparation has provided support for both general configuration and switch-specific accounts (Karayanidis et al., 2010). For example, Karayanidis et al. (2011) found that performance was significantly related to dissociable early and late ERP components that were either switch-specific (early) or observed in both repeat and switch trials (late; Karayanidis et al., 2011). Support for a switch-specific account has also been corroborated by evidence suggesting that early cue-locked ERP positivities are specifically linked to switch trial preparation (Karayanidis et al., 2009; Kieffaber and Hetrick, 2005), as well as to the need to switch away from the current task set in the absence of information specifying the forthcoming task set (Karayanidis et al., 2009). These findings support a model of task switching preparation that involves both general and specific configuration processes.

These findings converge with the results of several fMRI studies showing both general- (Barber and Carter, 2005; Brass and von Cramon, 2002; Gruber et al., 2006; Luks et al., 2002; Ruge et al., 2005; Ruge et al., 2009) and switch-related activity (Brass and von Cramon, 2004; Kimberg et al., 2000; Slagter et al., 2006; Sohn et al., 2000; Wylie et al., 2006). However, the locations of these switch-specific regions have varied across studies (e.g. dorsolateral prefrontal cortex, ventrolateral prefrontal cortex, superior parietal cortex) leading some to believe that multiple sources of control may exist (c.f. "multiple preparatory mode" hypothesis in Ruge et al., 2011).

This variation in the location of switch-specific activity across fMRI studies may be related to several factors including the poor temporal resolution of the technique or a lack of sensitivity to subtle differences in underlying signal due to high statistical threshold requirements (e.g. to avoid statistical false-discovery). However, a recent review by Ruge et al. (2011) has argued that a key distinction in understanding task switching preparation is specifying the components of the switching process that are potentially configured in advance (Ruge et al., 2011). For example in the letter-digit paradigm, it would be important to account for whether advance preparation served to benefit pre-target activation of the abstract task goal (e.g. "vowel/consonant" vs "odd/even" judgment), stimulus set (e.g. "attend letter" vs "attend digit"), or response rule set (e.g. "button 1 = vowel and button 2 = consonant" vs "button 1 = odd and button 2 = even"). If switch-specific activity was observed in a conflated design, in theory, control could be relegated to any of these component processes.

Fortunately, several fMRI studies have specifically focused on component processing during task switching (see Bunge et al., 2003; Chiu and Yantis, 2009; Esterman et al., 2009; Hyafil et al., 2009; Kim et al., 2011, 2012; Ravizza and Carter, 2008; Shi et al., 2011; Wager et al., 2005). While there is a general agreement across studies that the posterior parietal cortex (PPC) is involved in the preparation of attentional set to lower-level stimulus features (e.g. stimulus location; Chiu and Yantis, 2009; Ravizza and Carter, 2008), there is considerable variability as to which cortical regions are implicated in preparing for shifts of response rule. For example, using a cross-modal fMRI and ERP approach, Jamadar et al. (2010) mapped the preparation of abstract task goals to the DLPFC and response rules to the PPC by correlating early and late ERP components during preparation with fMRI activation (Jamadar et al., 2010). In contrast, other studies have implicated the involvement of the LPFC and regions surrounding the dorsal anterior cingulate (ACC) for switches in the response rule set (e.g. Bunge et al., 2003; Rushworth et al., 2002; Shi et al., 2011).

It is initially unclear why preparation for response rules would differ to such a degree across studies. However, one hint has been recently provided by a study that sought to dissociate rule set update from task goal preparation (Shi et al., 2011). In their study, Shi et al. (2011) evaluated preparation of response rules by comparing activation elicited by instructional cues informative of the task goal with cues that were informative of only the relevant response rules. In doing so, they demonstrated that several prefrontal regions, including the LPFC and pre-SMA (a region just superior to the ACC)



Fig. 1 – Experimental stimuli and procedure. (A) PERCEPTUAL task, shape trial, (B) RULE task, letter trial, (C) Example trial time-course with 500 ms CTI, 2500 ms of a RULE task letter trial, a 1000 ms post-trial fixation, and an n+1 1000 ms CTI shape (in this case a switch) cue.

were responsible for preparing the response rule. However, when the instructional cue indicated only the relevant task set, greater activity in these regions was subsequently elicited during target presentation signifying that while preparation of the relevant response rule may have begun, advance configuration was not complete before target onset. Taken together these studies indicate that when an instructional cue conveys task goal information, activation of the relevant task goal may nearly coincide with and occlude isolation of response rule preparation.

Given that computational models of cognitive control in task switching also suggest that response rules and stimulus sets may be inextricably bound to abstract task goal representation (c.f. Ruge et al. 2011; e.g. Brown et al., 2007; Meiran et al., 2008; Rubinstein, Meyer, and Evans, 2001), the poor temporal resolution of fMRI may cause the technique to be relatively insensitive to isolating component preparation. In order to control for this potential confound, we compared component processing in two conditions where task goals stayed constant. Specifically, we modified the Odd-Man-Out (OMO) task (Ravizza and Carter, 2008) to independently observe the preparation of response rules and stimulus-related attentional biasing under conditions constrained for switches in abstract task goal. Previously, we demonstrated that switching between univalent feature sets (i.e. letters or shapes) while performing singleton (OMO) identification incurs no shift-cost, suggesting that a switch in the specific feature dimensions in this task does not constitute a switch in stimulus set (Ravizza and Carter, 2008). However, adding a unique response rule for each feature set (see RULE task below) or creating interference by including an irrelevant stimulus feature in the stimulus display (i.e. bivalent stimulus sets, see PERCEPTUAL task below) resulted in significant shift-cost for each condition, and neurally dissociable loci of control (Ravizza and Carter, 2008). In our previous fMRI study (Ravizza and Carter, 2008), dissociable switch-related neural activation was observed in the lateral

prefrontal (response rule switch) and posterior parietal (stimulus set switch) cortices.

Thus, we reasoned that if response rules and stimulus sets are prepared in advance of target presentation, then preparation of each component would also be supported by such dissociable regions of control. By evaluating preparation for changes of response rule and stimulus set in the absence of a switch in task goal, we expected that the methodology would be sensitive to the isolation of respective control mechanisms. We predicted that if preparation of response rules or stimulus sets was switch-specific, then activity during preparation would be reliably greater for switch than repeat trials and shift-cost would be negatively related to neural activity. Additionally, given the results of our previous study (Ravizza and Carter, 2008), we predicted that advance configuration of response rules and stimulus sets would be implemented by dissociable neural regions (LPFC and PPC respectively).

2. Results

2.1. Behavioral results (response-time)

For RT analyses, only trials with correct responses were included. Note that there were no responses for catch trials as only cues were presented. A 2×2 repeated-measures ANOVA including trial-type (repeat and switch) and CTI (short and long) was performed on RT data for each task separately (see Fig. 2 for RT data).

2.1.1. RULE task

A significant main-effect of trial-type was observed (F(1,18) = 9.14, MSE=41448, p=0.007) where repeat trials were overall faster than switch trials, and a significant interaction between trial-type and CTI was observed (F(1,18)=9.46, MSE=44321, p=0.007). No significant main-effect of CTI was observed (F(1,18)=1.01, MSE=2884, p=0.33). The significant interaction was characterized by a significant reduction in RT with increase in CTI for switch-trials (t(18)=3.25, p=0.004), while RT for repeat trials did not significantly change with increase in CTI (t(18)=-1.7, p=0.11). A significant shift-cost of 95 ms was observed during short CTI trials (t(18)=4.38, p<0.001) that was abolished (-2 ms) at the long CTI (t(18)=0.07, p=0.94).

2.1.2. PERCEPTUAL task

A significant main-effect of trial-type was observed (F(1,18) = 6.81, MSE=57475, p=0.018) where repeat trials were overall faster than switch trials, and a significant main-effect of CTI was observed (F(1,18)=18.3, MSE=76034, p<0.001) where long CTI trials were overall faster than short CTI trials. No significant interaction between trial-type and CTI was observed (F(1,18)=2.5 MSE=8179, p=0.131). A non-significant 34 ms shift-cost was observed for short CTI trials (t(18)=1.34, p=.198) and a significant 76 ms shift-cost was observed for long CTI trials (t(18)=3.15, p=0.006).

2.2. Behavioral results (accuracy)

Due to near ceiling performance in all conditions, arcsine transformations were first performed on all accuracy proportion data in order to normally distribute mean accuracy



Fig. 2 – Mean response time for repeat and switch trials as a function of CTI. (A) RULE task: shift-cost reduced from 95 ms to –2 ms as CTI increased, (B) PERCEPTUAL task: shift-cost increased from 34 ms to 76 ms as CTI increased, primarily driven by a greater reduction of repeat RT than switch RT.

Table 1 – Significant clusters of activation from fMRI contrasts.						
Brain region/contrast	BA	# of voxels	Z- max	MNI coordinates		
				Х	Y	Z
PERCEPTUAL-Catch > Baseline						
R IFG/R Insula	44/47	2807	6.83 [†]	42	8	34
R Cuneus	17/18	823	5.97†	8	-104	2
R Angular gyrus/R IPL	39/40	540	4.99†	36	-58	40
R MTG	21/37	444	4.71 [†]	60	-48	6
L Angular gyrus/L IPL	39/40	330	4.99†	-26	-56	34
RACC	32	280	4.36†	12	14	44
R PCC	23	279	4.06	8	-24	24
L Fronto-occipital fasciculus	-	107	3.8	-26	-26	26
R MFG	46	106	3.68	30	56	16
L Cuneus	17/18	32	4.6†	-12	-102	2
RULE-Catch > Baseline						
R IFG/R Insula	44/47	1986	6.13 [†]	38	8	30
L Angular gyrus/L IPL/L	39/40	1569	5.41 ⁺	-28	- 56	36
fronto-occipital fasciculus						
R Cuneus	17/18	935	6.73 [†]	8	-104	2
R PCC	23	885	5.83†	2	-26	22
R Angular gyrus/R IPL	39/40	417	4.89 [†]	34	- 58	38
R ACC	32	186	4.08	10	14	48
R MTG	21/37	150	3.93	58	-48	6
L Cuneus	17/18	105	5.23 [†]	-12	-102	2
L Insula ^a	47	55	4.33 [†]	-30	28	-2
R MFG	46	48	3.79	28	56	16
RULE-Catch Switch > Repeat						
L IFG/MFG	45/46	197	3.56	-40	30	18
L pIFG	44	132	3.49	-44	8	18
L ACC	32	52	3.51	-4	22	40

^a L Insula was the only region active for RULE-Catch > Baseline but not for PERCEPTUAL-Catch > Baseline.

[†] Indicates that an ROI includes voxels that survive a voxel-wise whole-brain FWE-corrected threshold, p<0.05.

proportion. A 2×2 repeated-measures ANOVA including trialtype (repeat and switch) and CTI (short and long) was performed on accuracy data for each task separately.

2.2.1. RULE task

No main-effect of trial-type (F(1,18)=1.77, MSE=55, p=.2) or CTI (F(1,18)=2.1, MSE=83, p=0.16) was observed. However, a marginal interaction between trial-type and CTI was observed (F(1,18)=4.12, MSE=103, p=0.058). This marginal interaction was characterized by a significant increase in accuracy for repeat trials with increase in CTI (t(18)=2.36, p=0.03) where no difference in accuracy was observed for switch trials across levels of CTI (t(18)=0.13, p=0.9).

2.2.2. PERCEPTUAL task

No significant main-effect of trial-type (F(1,18)=1.02, MSE=66, p=0.326), CTI (F(1,18)=0.85, MSE=24, p=0.37), or interaction between trial-type and CTI (F(1,18)=1.52, MSE=68, p=0.23) was observed for PERCEPTUAL task accuracy data.

2.3. fMRI results

2.3.1. Switch-specific configuration

Regions thought to engage in advance reconfiguration should show switch-specific activity. To identify regions that exhibit increased activity during preparation for switch trials, contrasts were performed between RULE-Catch Switch > Rule-Catch Repeat and PERCEPTUAL-Catch Switch > PERCEPTUAL-Catch Repeat. The contrast of RULE-Catch Switch > RULE-Catch Repeat yielded three significant clusters of activation: 1) the Anterior Cingulate (ACC, BA 32), 2) the anterior aspect of the left Inferior Frontal Gyrus (L IFG/MFG, BA 45/46), and 3) the posterior aspect of the left Inferior Frontal Gyrus (L pIFG, BA 44), see Table 1 for peak voxel-coordinates. The pattern of activation in the ACC and L LPFC regions was such that all three regions exhibited increased activation during RULE-Catch Switch trials relative to RULE-Catch Repeat, as well as both PERCEPTUAL-Catch Repeat and Switch trials.

No significant clusters of activation were present in the contrasts of PERCEPTUAL-Catch Switch > PERCEPTUAL-Catch Repeat, RULE-Catch Repeat > RULE-Catch Switch, or PERCEPTUAL-Catch Repeat > PERCEPTUAL-Catch Switch at the chosen threshold, or at a more liberal voxel-wise significance threshold of p < 0.005 (Fig. 3).

As is the case with any study of task-switching effects, shift-costs were variable across participants, and to follow up on the hypothesis that activity in these regions facilitates preparation for RULE-switches correlations were performed between shift-cost for long CTI RULE task trials (i.e. prepared trials) and percent signal-change estimates extracted from



Fig. 3 – Whole brain contrast of RULE-Catch Switch > RULE-Catch Repeat. (LEFT) Significant clusters of activation were observed in the L ACC (BA 32) and two clusters in the L IFG (BA 44 and BA 45/46). Images are axial and sagittal view slices of z-statistic maps displayed over MNI standardized T1 template in radiological view, thresholded at z > 3.1, p < 0.001, k > 10. (RIGHT) Mean percent signal-change values for significant clusters of activation in the RULE-Catch Switch > RULE-Catch Repeat contrast: (A) ACC (BA 32), (B) L IFG/MFG (BA 45/46), (C) L pIFG (BA 44). All three regions behaved similarly, with each region being more active in RULE-Catch Switch than the other three conditions, but not differentially activated by PERCEPTUAL-Catch trials.



Fig. 4 – Correlation between activation in the ACC during RULE-Catch Switch trials and RULE task long CTI shift-cost. A negative correlation was observed between activation in the ACC during RULE-Catch Switch trials and shift-cost for prepared RULE task trials.

the contrast of RULE-Catch Switch > RULE-Catch Repeat. A significant correlation was observed between ACC activation during RULE-Catch Switch trials and shift-cost for prepared trials (r=-0.47, p=0.04, see Fig. 4). No correlation was observed between shift-cost and activation in the L IFG/MFG (r=-0.23, p=0.35) or the L pIFG (r=-0.24, p=0.32). Importantly, ACC and L IFG activation during the PERCEPTUAL-Catch Switch trials did not correlate with long CTI PERCEPTUAL task shift-cost (p>0.4 for all three tests). These results suggest that the ACC is associated with a reduction in shift-cost for prepared trials, and is specific to response rule component preparation.

It is important to note that the behavioral data (shift-cost) subjected to off-line correlation was observed during trials (cue+target) independent from the trials that percent signalchange estimates were acquired (cue-only). Thus, these tests do not suffer from statistical non-independence (Poldrack and Mumford, 2009).

2.3.2. General configuration

Several regions were equally active during preparation for both repeat and switch trials, supporting the contention of general configuration models that many common processes are configured in advance. Ten overlapping regions were significantly more active than baseline during preparation across both tasks and trial-types (see Table 1 and Fig. 5). To observe whether any of these regions showed domainspecificity, follow-up tests were performed comparing each task to baseline. The L Insula survived the contrast of RULE-Catch > Baseline but not the PERCEPTUAL-Catch > Baseline contrast. While the L Insula was significantly more active during RULE-Catch trials than baseline, this ROI was not significantly more active in RULE-Catch trials than PERCEPTUAL-Catch trials suggesting that it may not be unique to RULE task preparation. No region was significantly more active for one task than the other.

3. Discussion

In the current study, we evaluated the preparation of two component processes in task switching, response rules (i.e. action sets) and stimulus feature set (i.e. attentional sets), while controlling for switches in abstract task goal. Our



Fig. 5 – Whole brain contrast of PERCEPTUAL-Catch > Baseline and RULE-Catch > Baseline. Overlapping regions of common activation were observed during catch-trials for both tasks.

findings suggest that many of the processes involved in preparation are shared by switches of response rules and stimulus set, and can be characterized as involved in a general configuration process. In addition to neural regions involved in general configuration, switch-specific preparatory activity was observed for switches of response rule. The ACC and left IFG were more active in RULE-Catch Switch than RULE-Catch Repeat trials during preparation to switch response rule-sets, but were not differentially engaged during stimulus set biasing. Moreover, ACC activation during cue-only trials was associated with a reduction in RULE task shift-cost. This observation suggests that advance preparation of response rules is possible, and may be controlled through ACC signaling, as implemented through a putative ACC-LPFC cognitivecontrol network (Cole and Schneider, 2007; Cole et al., 2010).

3.1. Isolating component preparation

Computational models of cognitive control in task switching suggest that response rules and stimulus sets may be inextricably bound to abstract task goal representation (c.f. Ruge et al. 2011; e.g. Brown et al., 2007; Meiran et al., 2008; Rubinstein et al., 2001). In the current study, we reasoned that by constraining switches at the level of the abstract task goal, our design would be sensitive to the preparation of response- and stimulus-related component processing. In a previous study (Ravizza and Carter, 2008), we introduced a version of the current experimental paradigm involving no advanced instructional cue. In the "baseline" condition, where participants had to switch OMO identification between univalent stimulus displays (i.e. only letters, or only shapes) with an intuitive location-based response rule, no shift-cost was observed despite the lack of a preparatory interval. We have taken this result to suggest that a switch in the lowlevel feature dimensions of "letters" or "shapes" does not constitute a unique processing stage. When a unique response rule was added to each feature dimension in this baseline task (e.g. RULE task) a significant shift-cost was then observed. The same was true of simply adding an irrelevant feature dimension to the display and maintaining the location based response rule (e.g. PERCEPTUAL task). Thus, while each task in the current and previous study represents two degrees of change from one another, and thus prohibits direct statistical comparison, they each represent one source of added processing cost as compared with this baseline task. Therefore, we characterize the results of the current study in the context of such a manipulation.

In the RULE task, knowledge of the forthcoming feature set allowed for pre-trial activation of the relevant response rule. Similar to previous work, an increase in medial frontal cortex (MFC, e.g. dorsal ACC) predicted trial preparedness ("high readiness" group in Ruge et al., 2009). Ruge et al. (2009) interpret the role of the dorsal ACC in their study as a signal source for general 'motor readiness' that strategically confers an advantage to several trial-types (e.g. incongruent and congruent trials). In their study, the high-readiness group activated the dorsal ACC to advance target trials (presenting the targets without cue-information as to which task to perform) supporting their general readiness interpretation (Ruge et al., 2009). In the current study, a general motor readiness interpretation may serve as a potential explanation of the response rule preparation effect observed, but requires further research to unravel the specific process that is 'readied' by preparation (e.g. category update, pre-motor planning, etc.).

Our design investigated preparation of response rules and stimulus sets while controlling for response-conflict. In our experiment, we assume that preparatory activity was not related to either anticipatory conflict related activation (i.e. error-prediction, Brown and Braver, 2005; or task decision conflict, Braverman and Meiran, 2010) because there is minimal response-conflict in the stimulus displays for either task. While it is possible that response-conflict could be induced because of a bias to respond to the spatial location of the OMO rather than to its arbitrarily-assigned S-R mapping, this would be true in both repeat and switch trials, and does not explain the greater ACC activity to switching. Moreover, incongruency effects have been shown to be independent from task switching (Meiran, 2000).

During the PERCEPTUAL task an overall reduction in RT with increased CTI was observed suggesting that cued preparation for where or how to allocate visuospatial attention is possible. Residual switch-cost (response-time cost that remains following a switch-trial with a long CTI) was not eliminated or reduced with longer preparation intervals, and additionally, there was no differential neural facilitation between switch and repeat cues. The reduction in both switch and repeat RT with increased CTI may be indicative of a general configuration benefit for both types of trials, i.e. participants are ready to deploy attention to the spatial location or feature of the relevant stimulus set (outside/inside or letter/ shape). However, the presence of the alternative feature set during the PERCEPTUAL task appears to drive exogenous stimulus-triggered interference resulting in the residual cost (Meiran et al., 2000; Wylie and Allport, 2000). In fact, switching between univalent stimulus sets while performing singleton identification does not incur a shift-cost (Ravizza and Carter, 2008). These results suggest that the shift-cost in the PERCEPTUAL condition is incurred when the stimuli are displayed (i.e. stimulus-driven exogenous interference), and preparation for this type of interference may not be sufficient.

Alternatively, this pattern of results may reflect that instructional cues in the PERCEPTUAL task were not processed semantically. Instead, participants may have used the cue as a simple warning signal (this may have either been done as a conscious strategy or resulted from learning that preparation was not facilitative). Previous work on "foreperiod" effects (Woodrow, 1914) suggests that RT for the longer CTI should be faster than the short CTI due to the greater predictably of the longer CTI cues; that is, if the target does not appear after 500 ms (the short CTI), then participants can predict that the target will appear in 1000 ms (the long CTI). Thus, it is possible that the pattern of RT results and the lack of switch-specific PPC activity in the PERCEPTUAL condition were due to a lack of semantic processing of the instructional cue.

3.2. ACC-LPFC and response rule update

Similar to studies of working memory (Owen et al., 2005; Wager and Smith, 2003), and conflict monitoring and resolution (Badre and Wagner, 2004; Botvinick et al., 2004; Milham and Banich, 2005; Sohn et al., 2007; van Veen et al., 2001) the ACC may serve as an important signal to update the contents of working memory, increase the activation of control signals elsewhere in the PFC and detect conflict between competing response rules. In the current study, the ACC was the only region during preparation to correlate with a reduction in shift-cost. In the context of the current study, the ACC may be responsible for detecting that the currently active response rule does not match the episodic value of the cue ('letter' or 'shape') thereby signaling the PFC to update the rule-set. This interpretation of the ACC's role in conflict detection during cue processing is a departure from the previous literature on conflict monitoring and resolution. Typically, the ACC is observed in response to the imperative stimulus- rather than cue-driven response competition (i.e. stimulus incongruency, Brown, 2009; Gilbert and Shallice, 2002; MacDonald et al., 2000; Waszak et al., 2003); and semantic competition, (Badre and Wagner, 2002; Milham et al., 2001; Milham et al., 2003; Weissman et al., 2003). In the current study, the ACC could be taken to signal update of the contents of working memory and may operate similar to the "change-detector" proposed by Brown and colleagues (2007) which monitors control of response rules across trials (Brown et al., 2007). Taken together with previous reports of conflict-detection, the implication of this observation for procedural models of cognitive control is that at least two control systems may exist: one that responds within a trial (i.e. target processing) and one that monitors conflict across trials (i.e. "change-detector," Brown et al., 2007).

While activation in the ACC during RULE task cue-only switch trials was associated with a reduction in shift-cost for prepared cue+target trials, activity in both left IFG clusters was not reliably associated with performance. The interpretation that both clusters in the left LPFC are involved in preparation is consistent with models of cognitive control and PFC function despite the lack of a correlation with behavior (Hazy et al., 2007; Koechlin and Summerfield, 2007; Miller and Cohen, 2001). If these lateral regions of the PFC are responsible for maintaining the representations necessary to implement cognitive control, their role may not be necessary to deploy pre-target, but rather to bias the state of information during target processing. In the current study, we may be capturing the result of this effect before target presentation where repeat cues receive less priority than switch cues. Thus, evaluation of the neural effects of preparation for task switching may be sensitive to differences in activation of lateral PFC regions according to whether control representations are maintained (repeated) or about to be updated (switched).

A follow-up analysis of the ACC and the two left LPFC regions revealed that activation within all three regions is positively correlated across participants (ACC and L MFG/IFG (r=0.62, p=0.005); ACC and L IFG (r=.75, p<0.001)), confirming that participants with increased ACC activation also showed increased left LPFC activation. Though not directly addressable in the current design, this pattern may reflect a network of connectivity that implements control over response rule switching beginning pre-trial (ACC) that is updated at trial onset (LPFC). Because we cannot assess the relationship between ACC activation during preparation with left LPFC activation during target presentation due to poor temporal resolution and methodological constraints, this question remains as the subject of future research.

It has been well established that demands associated with target processing (e.g., stimulus incongruency) can impact task-switching behavior (Brown, 2009; Gilbert and Shallice, 2002; Koch and Allport, 2006; Meiran et al., 2008; Waszak et al., 2003). Therefore, a distinction between control at the level of advance preparation and control over target processing is integral. We argue that the negative association between ACC activation and shift-cost is indicative of a proactive preparatory process. To the degree that this process can also be observed during cue + target processing, we might also expect activation of the ACC (and also possibly both left LPFC regions) during cue+target trials to be associated with RT. A follow-up analysis suggests that while activation in all three regions during cue+target trials is marginally related to shift-cost (r-values between .3 and .4, p>0.13), we may not have sufficient power to detect such a relationship with 19 participants. One potential factor prohibiting us from being sensitive to this relationship may be that each of these regions exhibits a two- to four-fold increase in signal-change during cue+target trials relative to cue-only trials (e.g. cueonly switch activity in ACC=.14% signal change, vs .28% for cue+target switch activity, similarly .21% vs .6% in L pIFG and .07% vs .27% in L IFG/MFG). This increase in activation is encouraging as it indicates that regions involved in preparation are also involved in reactive control processes during target presentation. However, their receptivity to other demands associated with target processing may cause the observed individual difference relationship between preparation and shift-cost to be less robust when evaluated during cue +target trials (c.f. Ruge et al., 2011).

Several recent studies have identified the existence of domain-independent (i.e. component-independent) neural regions of controlled processing (Chiu and Yantis, 2009; Esterman et al., 2009). Similar to the OMO task, these studies utilized task switching paradigms that constrain switch-trial demand to one or another component at a time. In evaluating neural activation patterns during target processing, rather than preparation, support for specific and common regions of component control has been generated (Bunge et al., 2003; Chiu and Yantis, 2009; Esterman et al., 2009; Hyafil et al., 2009; Karayanidis et al., 2010; Kim et al., 2011, 2012; Ravizza and Carter, 2008; Wager et al., 2005). This phenomenon is replicated across studies on the control of advance preparation when components have been conflated in the design (Barber and Carter, 2005; Brass and von Cramon, 2002, 2004; Gruber et al., 2006; Kimberg et al., 2000; Luks et al., 2002; Ruge et al., 2005; Ruge et al., 2009; Slagter et al., 2006; Sohn et al., 2000; G. R. Wylie et al., 2006), and once again in the current study where components were isolated. It remains unclear whether the variability in identifying common and specific neural regions across studies is caused by the variability in the task switching paradigms chosen to explore preparation. However, as has been proposed by Ruge et al. (2011) we would argue that the variability is likely due to the information available in the instructional cue and the degree to which information bears

on the specific component "preparatory mode." In the current tasks, the cues used to prepare for stimulus set and response rule shifts are visually identical across the two tasks (the cue word "letter" was used in both tasks); however, this study provides evidence that they afford different levels of preparatory action.

3.3. Catch-trials

Isolation of preparatory activity in the current study was accomplished through the use of cue-only trials ("catch-trials"). This catch-trial methodology has been utilized by several previous studies on advance preparation (Brass and von Cramon, 2002; Slagter et al., 2006; Wylie et al., 2006); however, a few finer points about the design are worthy of consideration. First, catch-trials were infrequent in each fMRI run, and might be expected to elicit an "odd-ball" type of response. However, given that repeat and switch catch-trials were equally probable we assume that any oddball activity evoked by these trials would be subtracted out during the critical contrast between trial-types (e.g. switch > repeat; c.f. Brass and von Cramon, 2002). Secondly, a recent critical evaluation of the typical fMRI designs used to evaluate cognitive control endorsed the catch-trial method as particularly sensitive to preparatory activation, and suggested that various methods (e.g. fast event-related and catch-trial) yield strikingly similar results despite the surface differences (Goghari and MacDonald, 2008).

Note however, that catch trials are similar to "nogo" trials in which participants must withhold a response. In this case, ACC/PFC activity during this interval might reflect the need to withhold the execution of a prepared task set (Jamadar et al., 2010) rather than rule set preparation. However, three points argue against this alternative explanation. First, ACC activity on catch ("nogo") trials was related to an RT benefit on prepared cue+target ("go") trials where no inhibition was necessary. Second, our interpretation that these three regions are associated with preparation and not response inhibition is supported by the fact that both mid-LPFC regions are left lateralized (as opposed to right in Aron et al., 2003, 2004), as well as clearly superior to the ventral LPFC and inferior to the dorsal LPFC regions described in studies of response inhibition during task switching (Jamadar et al., 2010). Third, our ACC and LPFC regions were observed in both cue+target ("go") and catch ("nogo") trials. Thus, this activity is most likely due to response rule preparation rather than response inhibition.

3.4. Conclusions

The results of this study support a combined general and controlled configuration account of task switching. Most regions were active during preparation of stimulus sets and response rules and were equally active during repeat and switch trials, which suggests that many of the processes involved in preparation are shared between repeat and switch trials (i.e. generally configured). However, we identified a potential source of specific cognitive control for the preparation of response rules in the ACC and the left LPFC by isolating rule preparation from that of stimulus sets in the absence of a switch in task goal. Activation in the ACC and left LPFC appears to subserve the preparation of response rules, where increased activation of the ACC predicts a reduction in shift-cost for prepared trials. In contrast, preparation of stimulus sets during the OMO task appears to only benefit from a general configuration process and may be subject to exogenous interference generated by the presence of task-irrelevant stimuli in target displays. Our fMRI results replicate the general configuration account of preparation for task switching provided by previous studies on advance configuration. However, by observing preparation for component processing while controlling for changes in the task goal, we were able to isolate a switch-specific source of preparatory control that confers an advantage to the advance preparation of response rules.

4. Experimental procedures

4.1. Participants

Participants were 20 healthy, right-handed, English-speaking, Michigan State University undergraduate and graduate students (11 M; 9 F), ages (M=21.47, SD=2.95, range=18–29). One participant was not included due to becoming claustrophobic in the scanner environment. Participants were paid for their participation in the study. The study was approved by the Michigan State University Institutional Review Board.

4.2. PERCEPTUAL Odd-Man-Out task

During the PERCEPTUAL task, participants were asked to identify the OMO among a 4-position stimulus display consisting of letters and shapes (see Fig. 1A). Once the OMO was identified, participants pressed a key on the response glove that corresponded to the stimulus location (index finger = position 1, middle = position 2, etc.). These task and response-rules remained constant in every trial. At each of the 4 positions, a compound stimulus was displayed that consisted of a letter and a shape. The OMO occurred on only one of the two stimulus dimensions so that perceptual interference was present, but not response competition (i.e. stimulus bivalency but not response bivalency). The letter and shape stimuli used in the PERCEPTUAL task were: 'n', 'v', 'i', and 'b', and 'cross', 'triangle', 'rhombus', and 'hexagon', respectively.

4.3. RULE Odd-Man-Out task

During the RULE task (see Fig. 1B), positions were occupied by only shapes or only letters for a given trial. Participants were asked to identify the OMO in the 4-position stimulus display by pressing the proper finger from a pair of memorized stimulus-response mappings learned before the task. The response rule set for the LETTER condition was: index [finger] = 's', middle = 'x', ring = 't', and little = 'c.' The response rule-set for the SHAPE condition was: index = 'circle', middle = 'diamond', ring = 'pentagon', and little = 'square.'

Ten runs consisting of 2 counterbalanced blocks (1 RULE/1 PERCEPTUAL) were performed while participants underwent fMRI scanning. Each run was separated by approximately 90 s of rest time. Each block began with the instruction to

perform the PERCEPTUAL task (the word "LOCATION") or the RULE task (display of the response mappings). These instructions were displayed on screen for the first 4 s of each block. Each trial in a run had a 50% probability of being a shape or a letter trial resulting in approximately 82 trials of each trialtype (i.e. RULE-repeat) over the course of the experiment. A 100% valid cue (the word 'shape' or 'letter') was presented at the bottom of the screen below a fixation cross prior to each trial at a variable CTI (500 ms [short] or 1000 ms [long]) and remained on the screen for the duration of the trial. CTI was varied to provide behavioral evidence that participants were utilizing the cue. The stimuli remained on the screen for 2500 ms during which time responses were recorded, and were followed by either a 500 or 1000 ms fixation cross (see Fig. 1C). Following a minimum of 2 task-trials, catch-trials were randomly presented. Catch-trials occurred on approximately 22% of all trials resulting in approximately 18 catchtrials per trial-type. They occurred only after a repeat-trial, and included a cue ('shape' or 'letter') for 500 or 1000 ms, but were immediately followed by 15000 or 15500 ms of fixation (time-locked to the cue-length for a total 16000 ms). Due to the long cue-cue interval between a catch-trial and the subsequent cue+target trial, RT for cue+target trials that followed catch-trials was not included in the behavioral analysis. Catch-trials were randomly positioned in a run of trials. This unpredictably ensured that participants would respond to catch-trials equivalently to their response to cues in complete task-trials.

4.4. Practice and fMRI Scan

Participants were given approximately 20 min of practice prior to performing the experiment in the scanner. Participants were given 80 practice trials of the rule mappings where they were required to identify a single letter or shape presented in the center of the screen with the appropriate finger-press, and received feedback after each trial as to the accuracy of their response. Participants were required to achieve 90% or greater accuracy in order to proceed to the scan session; all participants met this requirement. Following the mapping practice session, participants were given one practice run of the task (i.e., a block of the RULE and a block of the PERCEPTUAL task) without trial by trial feedback to become accustomed to the procedure. Immediately following practice participants were given feedback on their performance on the task practice run, and began their fMRI scan.

4.5. Image acquisition

MRI data acquisition was performed on a 3 T GE Signa Scanner. Functional data were collected with a Blood Oxygenation Level Dependent (BOLD) echo-planar imaging (EPI) sequence (TR/TE=2000/27.7 ms, FOV=220 mm, matrix=64×64, slice-thickness/gap=3.4/0 mm). For anatomical reference, registration of functional data, and for normalization of functional data to a standard T1 template (Montreal Neurological Institute, MNI) a T1 magnetization prepared, rapid-acquisition gradient echo (MPRAGE, TR/TE=11.876/5.012 ms, FOV=240 mm, matrix=192×256, slice-thickness/gap=1.5/0 mm) sequence was used to collect a high-resolution image of the

participant's brain. Task stimuli were presented via E-Prime (version 2.0, Psychology Software Tools, Inc., Pittsburgh, PA) onto a 32-inch LCD monitor (Salvagione Design, Sausalito, CA) and reflected to the participant's visual field with a head-coil mounted mirror. Button-responses were logged with a BrainLogics Fiber Optic Response System glove (Psychology Software Tools, Inc., Pittsburgh, PA).

4.6. Imaging analysis

4.6.1. Preprocessing

fMRI and MRI data were preprocessed and analyzed using FMRIB's Software Library (FSL) fMRI Expert Analysis Tool (FEAT) (Smith et al., 2004). Functional data were brainextracted (Smith, 2002), motion-corrected to the median functional image using b-spline interpolation (4 df), high-pass filtered (60 s/cycle), and spatially smoothed (9 mm full width at half maximum (FWHM), isotropic). The anatomical volume was brain-extracted and registered to the standard space T1 MNI template using tri-linear interpolation with FMRIB's Linear Image Registration Tool (FLIRT, 12 df; (Jenkinson and Smith, 2001)). The median functional image was registered to the anatomical volume, and then transformed to the MNI template.

4.6.2. Subject analysis

Statistical images were created using FEAT with an improved General Linear Model (GLM (Smith et al., 2004)). Regressors were created by convolving binary time-course files for each condition with a canonical hemodynamic response function (HRF). Time-course files were generated separately for switch and repeat trials of each cue+target trial condition (RULE Repeat, RULE Switch, PERCEPTUAL Repeat, PERCEPTUAL Switch), as well as for each type of cue-only trial (RULE-Catch Repeat, RULE-Catch Switch, PERCEPTUAL-Catch Repeat, PERCEPTUAL-Catch Switch). For purposes of imaging analysis, cue+target trial conditions were collapsed across 500 ms and 1000 ms CTI lengths as the 500 ms variation in CTI was not sufficient to resolve differences between conditions after convolution with the HRF. Each regressor was entered into the GLM along with their temporal derivative and 6 motion parameters (motion in x, y, z, roll, pitch, and yaw).

4.6.3. Group analysis

Parametric maps for Catch Switch and Repeat trials were averaged and contrasted with baseline for each task separately in order to evaluate for non-zero common regions of activation during preparation. Paired-samples one-way t-tests were performed in a second-level GLM to contrast catch-trial activity with baseline activation levels.

Paired-samples t-tests were performed in a second-level GLM to contrast cue-only switch and repeat activity for each task separately. Contrasts were performed between RULE-Catch Switch and RULE-Catch Repeat as well as PERCEPTUAL-Catch Switch and PERCEPTUAL-Catch Repeat. For all within-subjects comparisons, individual subject betaimages were entered along with a regressor per subject to account for subject-specific variance. Group analyses were performed using FSL's FLAME stages 1 and 2 higher-level analysis tool (Woolrich et al., 2009), and all F- and T-statistics were converted to unit-normal Z-statistics. 4.6.4. Cluster definition/percent signal-change

Functional ROI's were defined by clusters surviving voxelwise thresholding at p<0.001 with a minimum extent of 10 contiguous voxels. For display, percent signal-change values for catch-trials were calculated by subtracting BOLD-signal values during the last 3 s of a catch trial from those obtained during the peak of the canonical HRF (3–7 s) following the onset of the trial. The resultant signal difference was converted to percent signal-change by dividing the difference by the timecourse average BOLD-signal.

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