Domain General and Domain Preferential Brain Regions Associated With Different Types of Task Switching: A Meta-Analysis

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Abstract: One of our highest evolved functions as human beings is our capacity to switch between multiple tasks effectively. A body of research has identified a distributed frontoparietal network of brain regions which contribute to task switching. However, relatively less is known about whether some brain regions may contribute to switching in a domain-general manner while others may be more preferential for different kinds of switching. To explore this issue, we conducted three meta-analyses focusing on different types of task switching frequently used in the literature (perceptual, response, and context switching), and created a conjunction map of these distinct switch types. A total of 36 switching studies with 562 activation coordinates were analyzed using the activation likelihood estimation method. Common areas associated with switching across switch type included the inferior frontal junction and posterior parietal cortex. In contrast, domain-preferential activation was observed for perceptual switching in the dorsal portion of the premotor cortex and for context switching in frontopolar cortex. Our results suggest that some regions within the frontoparietal network contribute to domain-general switching processes while others contribute to more domain-preferential processes, according to the type of task switch performed. *Hum Brain Mapp 33:130–142, 2012.* © **2011 Wiley Periodicals, Inc.**

Key words: cognitive control; brain imaging; task switching; meta-analysis; switch type; perceptual switching; response switching; context switching

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INTRODUCTION

Cognitive control refers to a set of processes that enable humans to flexibly coordinate thoughts and behaviors in order to accomplish internal goals [Miller and Cohen, 2001]. An important component of cognitive control

involves the ability to reconfigure task sets in a flexible manner in order to meet shifting demands [Monsell, 2003]. One of the most common ways to explore this cognitive ability is through the use of the task switching paradigm, in which a participant's reaction time (RT) is compared when they switch between performing two simple tasks versus performing either task alone [Jersild, 1927]. The requirement to switch between performing two tasks results in a RT increase compared with performing either task in isolation, termed a switch cost [Kramer et al., 1999; Rogers and Monsell, 1995].

Functional neuroimaging studies have identified a distributed frontoparietal network of brain regions which contribute to task switching. Within the frontoparietal network, there appear to be several key cortical hubs that are active across a variety of stimuli and paradigms including dorsolateral prefrontal cortex (DLPFC), ventrolateral prefrontal cortex (VLPFC), frontopolar cortex (FPC), and

posterior parietal cortex (PPC) [e.g., Badre and Wagner, 2006; Braver et al., 2003; Crone et al., 2006; Dove et al., 2000; Gold et al., 2010; Liston et al., 2006; Sohn et al., 2000]. However, less is known about whether some of these regions may contribute to switching in a domain-general manner whereas others may be more preferential for different kinds of switching. One reason for this knowledge gap is that neuroimaging studies have tended to describe switching as a unitary process, with limited consideration of the potential role of switch type on brain activation patterns.

Nevertheless, a few neuroimaging studies that have directly compared different switch types have tended to report distinct neural correlates associated with different switch types [Nagahama et al., 2001; Ravizza and Carter, 2008; Rushworth et al., 2002]. For example, Ravizza and Carter [2008] tested whether neural networks are dissociable when switching between perceptual features or between response rules. These authors found that DLPFC (BA 9/46) showed greater activity for response switching than for perceptual switching while the dorsal premotor cortex (BA 6) showed greater activity for perceptual than response switching.

Such findings raise the question of whether some regions within the frontoparietal task switching network may be relatively specialized for particular kinds of task switches. The present meta-analysis was conducted to explore this issue. Specifically, we aimed to test whether some frontoparietal brain regions contribute to task switching irrespective of the kind of switch being performed, whereas others may be preferential for the type of switch being performed. A meta-analysis is appropriate to address this question because it incorporates results obtained from different scanners, participants, and statistical analysis approaches and is thus insensitive to idiosyncracies associated with any one study. In surveying the literature, we identified three distinct switch types that have been employed frequently in studies of task switching: perceptual, response, and context.

Perceptual switching refers to switching attention between perceptual features of a stimulus or between stimulus selection rules in order to make a task-appropriate decision about the properties of a stimulus. For example, subjects are instructed to respond based on shape (e.g., a circle indicates a left button press, and a square indicates a right button press), or to respond based on the direction of an arrow (e.g., a left pointing arrow indicates a left button press and a right pointing arrow indicates a right button press). The defining feature of perceptual switching is that attention must be actively switched between perceptual features (i.e., shape and direction) in order to select the appropriate, task-relevant response.

Response switching refers to switching between two or more arbitrary or opposing S-R mappings (sometimes called S-R reversal paradigms). In a typical response switching task, participants may be asked to select the higher of two numbers, with the S-R mappings depending upon a cue. For example, a red color cue might indicate that the left button is associated with a lower digit whereas the right button is associated with a higher digit. Conversely, a green color cue might indicate that the left button is associated with a higher digit and the right button is associated with a lower digit. To perform accurately participants must maintain two arbitrarily assigned S-R contingencies in mind and actively switch between them based on a cue.

Context switching (sometimes called set shifting) refers to shifting between task rules or cognitive sets. A prototypical context switching task is the Wisconsin Card Sorting Task (WCST), which has been used in the study of patients with PFC lesions [e.g., Nelson, 1976; Stuss et al., 2000] and in many functional neuroimaging studies [e.g., Monchi et al., 2001; Nagahama et al., 2001; Rogers et al., 2000]. On the WCST, a participant is instructed to match a target card to one of four simultaneously presented cards, according to one out of three possible matching rules (i.e., color, shape, or number of stimuli). The participant is not told how to match the cards but is informed whether a particular match is correct or incorrect following each trial. Thus, context switching emphasizes endogenous control processes associated with the maintenance and switching between multiple cognitive sets.

In the present study, we first conducted a meta-analysis of switching studies collapsed across each of these three switch types to identify the broad network of brain regions that contribute to task switching. We then performed three separate meta-analyses to identify the broad network of regions that contribute to each switch type. Next, a conjunction map was created from these individual meta-analyses to identify domain-general switch regions. Finally, we carried out three additional meta-analyses focusing on direct comparisons between switch types to identify regions which contribute to specific switch types in a domain-preferential manner.

METHODS

Selection of Studies and Contrasts of Interest

In our meta-analyses, we included functional neuroimaging switching studies (fMRI or PET) published in English between the years of 1995 and 2009. These studies were identified via searches on Medline and PsycInfo. Studies were included if they reported whole-brain comparisons of switching tasks in which the control task required processing stimuli of similar complexity and similar motor output as the switch task (i.e., switch vs. nonswitch trials but not switch vs. passive fixation or rest baselines). We considered studies involving healthy, young adults. For the studies in which young adults were compared to older adults or young adults were compared with patients, we included only the results from the healthy, young adults. For fMRI studies, both block and event-related designs were included.

We included only studies that reported peaks of activation in standardized coordinate space (Talairach or MNI) based on group analyses. We excluded studies that used emotional stimuli in the tasks. All studies meeting these inclusion criteria were reviewed independently by each of the authors to determine switch type designation (using criteria described in the Introduction section for each of the switch types). Only studies in which the authors unanimously agreed upon the switch type designation were included in the reported analyses. Using these criteria, we were able to identify 48 studies. Among these studies, 12 studies were excluded since these studies involved multi-dimensional kinds of switching (i.e., both perceptual and response switching). As a result, 36 studies were included in this study (see Table I for details).

Activation Likelihood Estimation Meta-Analyses

For the meta-analyses, we used GingerALE 1.2 in conducting activation likelihood estimation (ALE) analyses for the contrasts of interest [Laird et al., 2005; Turkeltaub et al., 2002]. The ALE method is a voxel-based meta-analysis technique used for a quantitative evaluation of the reliability of spatial patterns of activation foci across independently conducted neuroimaging studies. The method yields a statistical map that indicates the set of brain voxels that are more active than would be expected by chance alone, using a permutation-testing framework to assess the extent to which the spatial location of activation foci are correlated across independently conducted studies. Each reported locus of maximal activation from each contrast was modeled as a center of a three-dimensional Gaussian probability distribution with a full-width half-maximum (FWHM) of 10 mm. For studies reporting MNI coordinates, a conversion tool [Lancaster et al., 2007] was used to convert the coordinates into Talairach space. Every three-dimensional Gaussian distribution from the set of studies contributed to create a statistical map to estimate the likelihood of activation in each voxel (2 mm^3 in Talairach space). ALE maps were then thresholded at $P < 0.05$ using the false discovery rate (FDR) method to correct multiple comparisons. Clusters exceeding 120 mm^3 (15 continuous voxels) were applied for all analyses. Thresholded ALE maps were overlaid onto the "colinbrain" Talairach template [Kochunov et al., 2002] using the MRIcron software (http://www.cabiatl.com/mricro/).

Four individual ALE analyses were performed: (1) all switch types (65 contrasts with 562 foci); (2) perceptual switching (24 contrasts with 119 foci); (3) response switching (21 contrasts with 156 foci); and (4) context switching (20 contrasts with 287 foci). The ALE analysis for all switch types included all of the above perceptual, response, and context switching foci. Details of these studies are shown in Table I. Additionally, three direct comparisons were performed. For the three direct comparisons, 118 foci were randomly selected per switch type in order to equate power. The direct comparisons were: (1) perceptual switching (118 foci) versus response (59 foci) and context switching (59 foci); (2) response switching (118 foci) versus perceptual (59 foci) and context switching (59 foci); and (3) context switching (118 foci) versus perceptual (59 foci) and response switching (59 foci). The 59 foci used in the direct comparisons were randomly selected from the total of 118 foci per switch type.

RESULTS

The results of the ALE analysis for all switching studies are shown in Figure 1. The results showed that switching was associated with a distributed network of brain regions including medial PFC (BAs 6 and 32), lateral PFC (BAs 6, 9, 46, and 10), and parietal (BAs 7 and 40), temporal (BA 37), and occipital cortices (BAs 18 and 19), as well as subcortical structures (caudate nucleus and thalamus).

The results of the individual ALE analyses for perceptual, response, and context switching contrasts are presented in Figure 2A. The ALE analysis of perceptual switching revealed activation of a distributed set of brain regions. Within frontal cortex, perceptual switching activation was observed in a rostral portion of the dorsal premotor cortex (pre-PMd; BA 6), anterior cingulate cortex (ACC)/pre-supplementary motor area (pre-SMA) (BA 32/6), inferior frontal junction (IFJ; BA 44/6/9). In addition, perceptual switching activations were observed in several posterior regions: PPC (BAs 7 and 40), and temporal and visual areas (BAs 37, 19, 18, and 17). The ALE analysis of response switching revealed a frontoparietal activation pattern. Specifically, we found activations in pre-SMA/ACC (BAs 6 and 32), inferior and middle frontal gyri (BAs 44, 45, 46, 9, 10, and 47), IFJ (BA 44/6), PPC (BAs 7 and 40), and precuneus. The ALE analysis of context switching also revealed activation of a frontoparietal network. Activation was observed in diverse PFC regions, such as lateral and medial FPC (BA 10), IFJ (BAs 6/44), inferior and middle frontal gyri (BAs 8, 9, 46, and 47), pre-SMA and ACC (BAs 6, 32, and 8). Additional activations were found in PPC, precuneus and cuneus (BAs 40, 7, and 19), and inferior temporal (BAs 19 and 37) and visual areas (BAs 18 and 19).

Using the above individual analyses, the conjunction map was calculated by taking the voxel-wise intersection of three individual ALE maps in order to identify common areas activated by perceptual, response, and context switching contrasts. As shown in Figure 2B, the left IFJ (BA 6/44; centered at −40, 3, 33) and PPC (BA 7; centered at −25, −68, 36) were the only regions that showed overlap of significant voxels across perceptual, response, and context switching.

The next analyses focused on direct comparisons between three switching contrasts in order to identify regions preferentially activated by each switch type. The results of the direct comparisons between switch types are

TABLE I. The list of switching studies included in the ALE meta-analyses

Author (year)	Method	N	Contrast	Task	Foci
Context switching					
Berman et al. [1995]	PET	40	Shifting > control	WCST	35
Braver et al. [2003]	fMRI	13	Mixed > single state	Semantic classification	3
Goldberg et al. [1998]	PET	12	Shifting > control	WCST	17
Graham et al. [2009]	fMRI	18	2+NF > 2 + PF	Modified WCST	14
Koechlin et al. [1999]	fMRI	6	Branching > control	Letter matching	2
Koechlin et al. [2000]	fMRI	6	Predictive and random > control	Letter matching	12
Konishi et al. [2002]	fMRI	16	Dimensional change > no-change	Modified WCST	9
Monchi et al. [2001]	fMRI	11	Shifting > control	WCST	30
Monchi et al. [2001]	fMRI	11	Shifting > no shifting	WCST	9
Monchi et al. [2004]	fMRI	9	Shifting > control	WCST	17
Monchi et al. [2004]	fMRI	9	Shifting > no shifting	WCST	6
Nagahama et al. [1997]	PET	6	MCST > number-matching task	MCST	26
Nagahama et al. [2001]	fMRI	6	Set shift > no-shift	Modified WCST	14
Nakahara et al. [2002]	fMRI	10	Shifting > maintenance	Modified WCST	13
Pollmann et al. [2000b]	fMRI	10	Dimension change > no change	Visual detection (odd one out)	16
Pollmann et al. [2000b]	fMRI	10	Cross-dimensional change > control	Visual detection (odd one out)	24
Rogers et al. [2000]	PET	12	Extra- > interdimensional shift	ID/ED task	4
Rogers et al. [2000]	PET	12	Extradimensional shift > reversal	ID/ED task	3
Weidner et al. [2002]	fMRI	10	Cross-dimension change > no-changes	Visual detection (odd one out)	16
Zanolie et al. [2008a]	fMRI	18	Extradimensional shift > no-shift	Modified ID/ED	17
Response switching					
Barber and Carter [2005]	fMRI	13	Switch > repeat (preparation phase)	S-R incompatibility task	1
Barber and Carter [2005]	fMRI	13	Switch > repeat (target phase)	S-R incompatibility task	4
Brass and von Cramon [2004]	fMRI	14	Meaning switch > cue switch	Digit discrimination	3
Crone et al. [2006]	fMRI	20	Bivalent switches > repetitions	Visual discrimination	23
Dove et al. [2000]	fMRI	16	Switch> repetition	Visual detection	13
Dreher et al. [2002]	fMRI	8	Switching > baseline (nonswitch)	Letter discrimination	9
Jancke et al. [2000]	fMRI	6	Switch > fixed task (repetitive)	Finger tapping	3
Jancke et al. [2000]	fMRI	6	Switch > fixed task (sequential)	Finger tapping	6
Luks et al. [2002]	fMRI	11	Informative cues > neutral cues	Digit discrimination	4
Luks et al. [2002]	fMRI	11	Neutrally cued switch > repeat targets	Digit discrimination	2
Luks et al. [2002]	fMRI	11	Switch > repeat targets	Digit discrimination	2
Nagahama et al. [2001]	fMRI	6	Response shift > no-shift	Modified WCST	13
Parris et al. [2007]	fMRI	22	Flip > hold	Switch response rules	20
Pollmann et al. [2000a]	fMRI	11	Switch > basic task	Visual detection	6
Pollmann et al. [2006]	fMRI	20	Change > stay (response)	Visual detection (odd one out)	15
Ravizza and Carter [2008]	fMRI	14	Shift > repetition (response rule)	Visual detection (odd one out)	4
Rogers et al. [2000]	PET	12	Reversal > interdimensional shift	ID/ED task	5
Rogers et al. [2000]	PET	12	Reversal > extradimensional shift	ID/ED task	3
Rushworth et al. [2002]	fMRI	10	Switch > stay	Visual detection	4
Sohn et al. [2000]	fMRI	12	Repetition and switch x scan	Letter-digit task	4
Zanolie et al. [2008b]	fMRI	20	Shift > no-shift	Location rule switch	12
Perceptual switching					
Brass and von Cramon [2004]	fMRI	14	Cue switch > cue repetition	Digit discrimination	4
Crone et al. [2006]	fMRI	20	Univalent switches > repetitions	Visual discrimination	2
Gurd et al. [2002]	fMRI	11	Switching > no switching	Verbal fluency	2
Liston et al. [2006]	fMRI	19	Shift > repeat (color and motion)	Visual detection	7
Liston et al. [2006]	fMRI	19	Shift > repeat (color)	Visual detection	2
Liston et al. [2006]	fMRI	19	Shift > repeat (motion)	Visual detection	2
Pessoa et al. [2009]	fMRI	20	Switch > nonswitch	Visual detection	8
Pessoa et al. [2009]	fMRI	20	Switch > nonswitch (color cue)	Visual detection	10
Pessoa et al. [2009]	fMRI	20	Switch > nonswitch (pop-out)	Visual detection	2
Pollmann et al. [2006]	fMRI	20	Dimension change > dimension stay	Visual detection (odd one out)	5
Ravizza and Carter [2008]	fMRI	14	Shift > repetition (perceptual)	Visual detection (odd one out)	5
Rogers et al. [2000]	PET	12	Interdimensional shift > reversal	ID/ED task	3
Rogers et al. [2000]	PET	12	Inter- > extra-dimensional shift	ID/ED task	6

TABLE I. (Continued)

Author (year)	Method	N	Contrast	Task	Foci
Rushworth et al. [2002]	fMRI	8	Switch > stay	Visual detection	
Serences et al. [2004]	fMRI	15	Switching > holding attention	Attention shift	5
Serences et al. [2004]	fMRI	8	Switching > holding attention	Attention shift	2
Vandenberghe et al. [2001]	fMRI	11	Shifting > maintaining	Spatial shift of attention	4
Weidner et al. [2002]	fMRI	10	Within-dimension change > no-changes	Visual detection (odd one out)	1
Wilkinson et al. [2001]	fMRI	12	Internal and external switch > no-switch	Visual discrimination	7
Wylie et al. [2006]	fMRI	13	Color switch > color repeat (cues)	Visual detection	11
Wylie et al. [2006]	fMRI	13	Speed switch > speed repeat (cues)	Visual detection	2
Wylie et al. [2006]	fMRI	13	Color switch > color repeat (targets)	Visual detection	19
Wylie et al. [2006]	fMRI	13	Speed switch > speed repeat (targets)	Visual detection	4
Zanolie et al. [2008a]	fMRI	18	Intradimensional shift > no-shift	Modified ID/ED	4

presented in Figure 3 and cluster details are listed in Tables II to IV. Preferential activation associated with perceptual switching was observed in caudal PFC regions, such as bilateral pre-PMd (BA 6), left middle frontal gyrus (BA 6), precentral gyrus (BAs 6 and 9), medial frontal gyrus (BA 6) and cingulate gyrus (BA 32). Additionally, PPC (BA 7) and inferior temporal areas (BAs 19 and 37) were also preferentially activated by perceptual switching contrasts.

Preferential activation associated with response switching was observed in a left mid-PFC region centered on DLPFC (BA 46). Other PFC regions, such as left superior frontal gyrus (BA 6), left precentral gyrus (BAs 6 and 44), right inferior frontal gyrus (BA 47), and medial frontal gyrus (BA 6), and bilateral PPC (BAs 7 and 40) regions were also activated by response switching.

Finally, preferential activation associated with context switching was observed in rostral PFC regions, such as lateral and medial FPC (BA 10) and ACC (BA 32). Context switching was also associated with activations in middle frontal gyrus (BAs 6 and 9), PPC (BA 7 and 40), cuneus (BAs 18 and 19), inferior temporal areas (BA 37), visual areas (BAs 18 and 19), and subcortical structures (thalamus and lentiform nucleus).
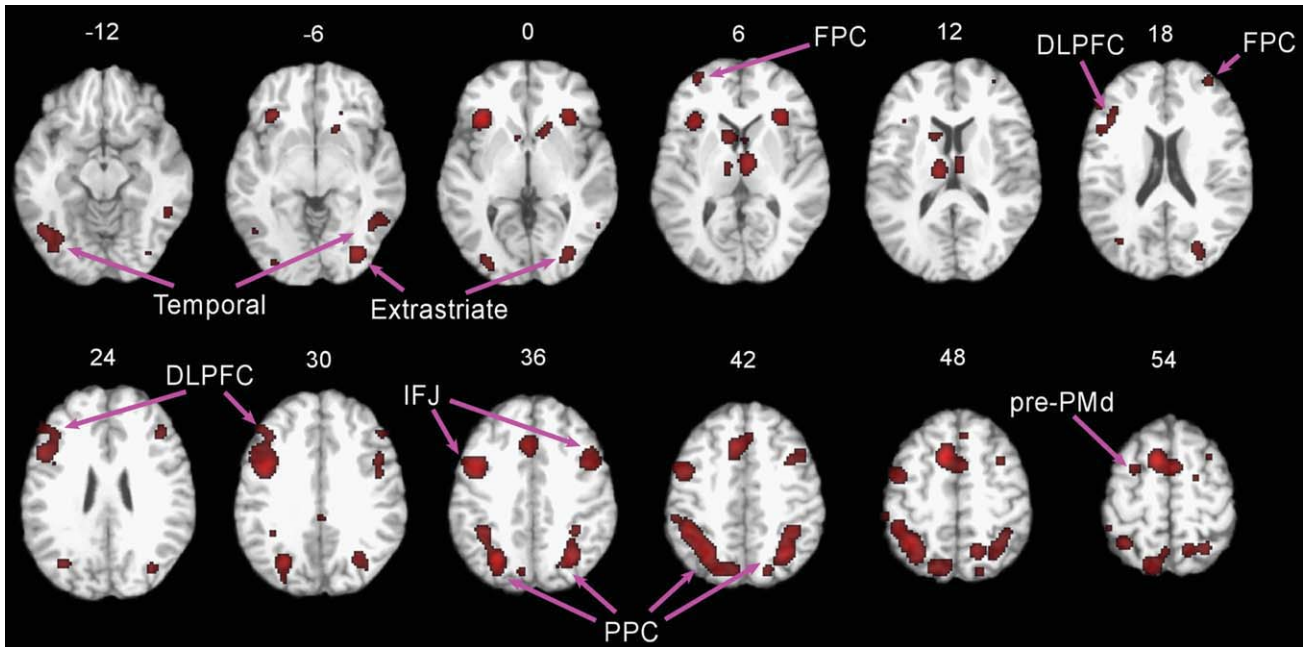

Figure 1.

Activations associated with task switching contrasts collapsed across switch type. The ALE activation map thresholded at $P < 0.05$ (corrected) is overlaid onto the "colinbrain" template. Numbers indicate z-coordinates of axial planes.
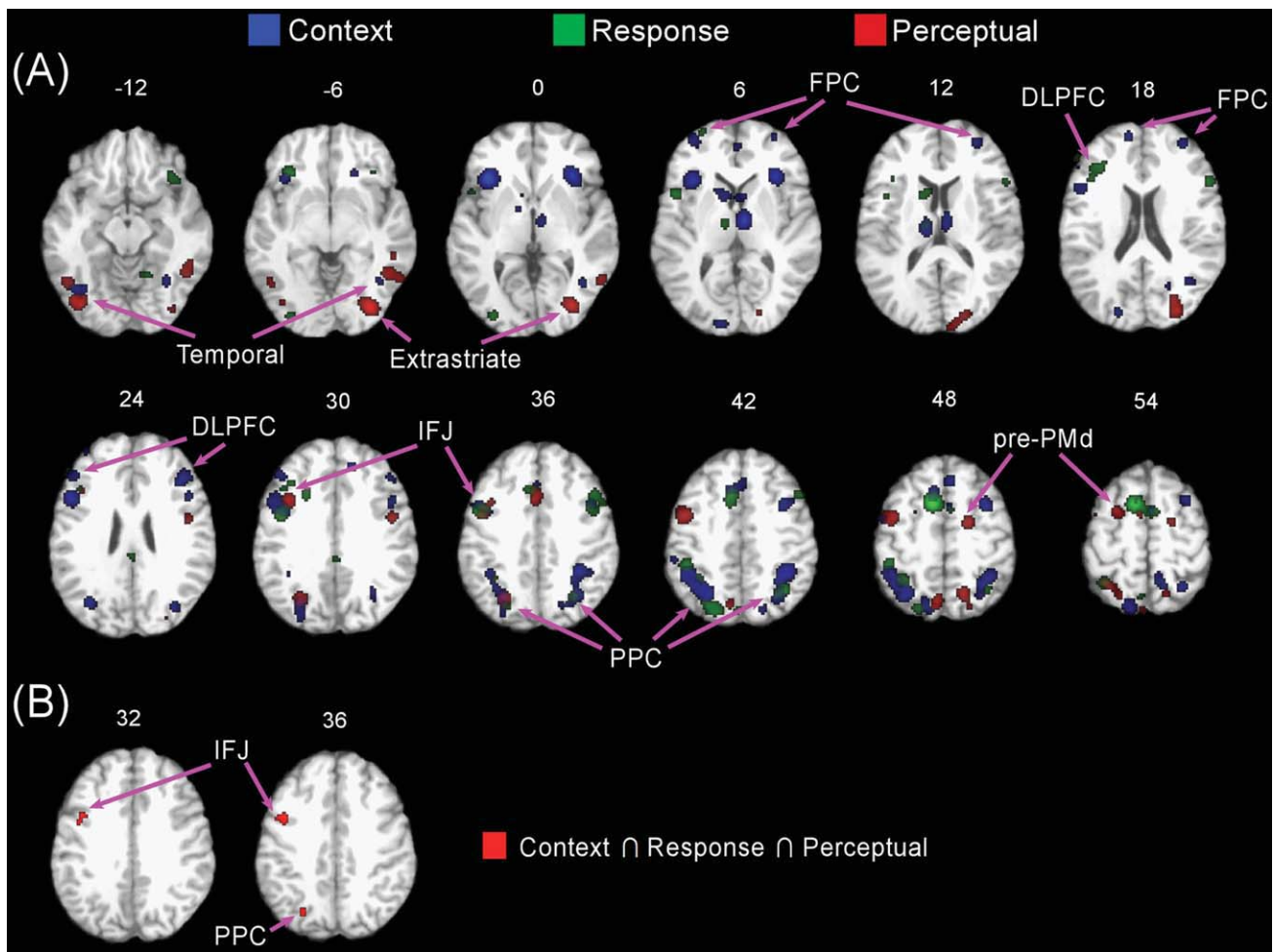
Figure 2.
Activations associated with each switch type and their conjunction. The ALE activation maps of separate context, response, and perceptual switching contrasts compared with nonswitching overlaid on a common "colinbrain" template (**A**). The conjunction of context, response, and perceptual switching contrasts (**B**). Numbers indicate z-coordinates of axial planes.

DISCUSSION

The current meta-analysis sought to distinguish brain regions within the distributed frontoparietal task switching network that contribute to switching in a domain-general manner from those that may be more specialized for different kinds of switching. Three switch types were explored which have been frequently used in the task switching literature (perceptual, response, and context). The results of the ALE meta-analysis that collapsed across all (perceptual, response, and contextual) switch types revealed a distributed frontoparietal network associated with switching. These results are consistent with those from previous meta-analysis studies that have collapsed

across distinct switch types [Buchsbaum et al., 2005; Derrfuss et al., 2005; Wager et al., 2004].

However, results from our meta-analyses also provide new evidence related to the on-going debate about the degrees of domain-specificity of brain regions within the distributed frontoparietal task switching network. We observed three main patterns in our meta-analyses: (1) regions exhibiting domain general patterns across all switching tasks (i.e., putative domain-general switch regions); (2) regions showing a pattern of clear domain preferentiality/specificity according to switch type (i.e., putative domain-preferential switch regions); and (3) regions showing an activation pattern that was preferential, but not selective, for one switch type. Below
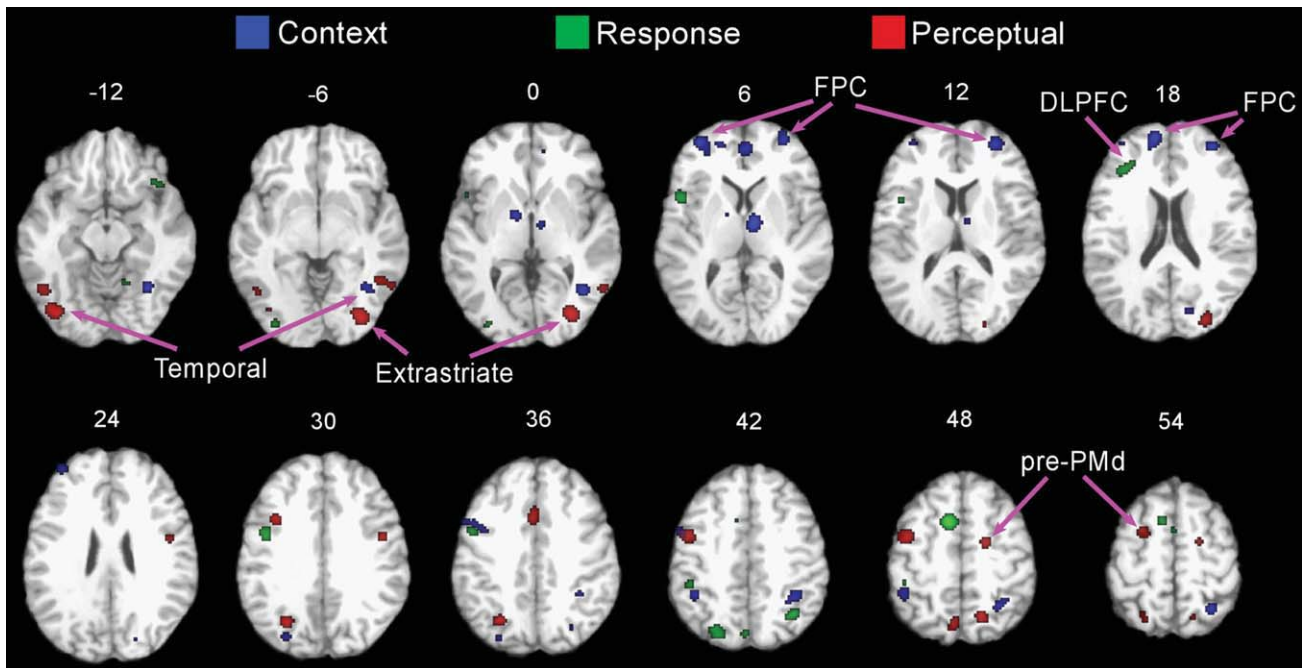
Figure 3.
Domain-preferential activations according to switch type. The ALE activation maps of three direct comparisons: (1) context switching versus response and perceptual switching; (2) response switching versus context and perceptual switching; (3) perceptual switching versus context and response switching. The activation maps thresholded at $P < 0.05$ (corrected) are overlaid onto the "colinbrain" template. Numbers indicate z-coordinates of axial planes.

TABLE II. Brain regions preferentially activated by perceptual switching compared to context and response switching

Region	Hem	Talairach			BA	ALE	Volume (mm³)
		x	y	z			
Middle frontal gyrus	L	−40	−2	48	6	0.0119	1,256
Pre-PMd	L	−22	2	54	6	0.0102	400
Pre-PMd	R	20	−6	50	6	0.0116	392
Precentral gyrus	R	46	−2	28	6	0.0111	384
Precentral gyrus	L	−36	10	30	9	0.0115	360
Medial frontal gyrus	L	−8	0	60	6	0.0096	312
Cingulate gyrus	L	0	14	34	32	0.0106	512
Precuneus	L	−26	−66	32	7	0.0153	632
Superior parietal lobule	L	−20	−66	58	7	0.0090	496
Precuneus	R	16	−62	50	7	0.0119	456
Precuneus	L	−4	−68	48	7	0.0097	384
Fusiform gyrus	L	−38	−78	−12	19	0.0138	912
Fusiform gyrus	R	48	−54	−8	37	0.0104	640
Inferior temporal gyrus	R	56	−58	−2	37	0.0096	SC
Fusiform gyrus	L	−46	−62	−10	37	0.0092	624
Inferior occipital gyrus	R	32	−80	−2	18	0.0165	1,320
Middle occipital gyrus	R	30	−84	20	19	0.0103	496

Hem, hemisphere; BA, Brodmann area; ALE, activation likelihood estimation; pre-PMd, the rostral portion of the dorsal premotor cortex; SC, same cluster.

TABLE III. Brain regions preferentially activated by response switching compared to context and perceptual switching

Region	Hem	Talairach			BA	ALE	Volume (mm^3)
		x	y	z			
Superior frontal gyrus	L	−8	10	48	6	0.0192	1,064
Precentral gyrus	L	−42	0	30	6	0.0101	640
Precentral gyrus	L	−48	10	4	44	0.0111	568
Middle frontal gyrus (DLPFC)	L	−34	30	18	46	0.0097	456
Medial frontal gyrus	R	2	2	58	6	0.0087	216
Inferior frontal gyrus	R	38	20	−12	47	0.0077	144
Inferior frontal gyrus	R	42	18	−10	47	0.0077	SC
Precuneus	L	−22	−74	44	7	0.0122	624
Inferior parietal lobule	R	36	−60	44	7	0.0113	368
Inferior parietal lobule	L	−44	−38	42	40	0.0090	232
Precuneus	L	−2	−76	40	7	0.0086	184
Inferior occipital gyrus	L	−32	−86	−4	18	0.0096	248
Cerebellum (declive)	R	16	−56	−14		0.0079	152

Hem, hemisphere; BA, Brodmann area; ALE, activation likelihood estimation; DLPFC, dorsolateral prefrontal cortex; SC, same cluster.

we discuss each of these three main patterns and their contribution to understanding the neural bases of cognitive control processes involved in task switching.

Domain-General Switching Mechanisms Within the Frontoparietal Network

Within the distributed network of frontoparietal brain regions associated with task switching, there were two regions, the inferior frontal junction (IFJ) and posterior parietal cortex (PPC), which were found to contribute to each of the three (perceptual, response, and context) forms of switching explored in our meta-analyses. The IFJ is a posterior lateral region of frontal cortex near the junction of the inferior frontal sulcus and the inferior precentral sulcus (~BA 44/6/9) [Derrfuss et al., 2004]. The PPC comprises a wide expanse of parietal cortex (~BA 40/7) including much of the inferior and superior parietal

TABLE IV. Brain regions preferentially activated by context switching compared to perceptual and response switching

Region	Hem	Talairach			BA	ALE	Volume (mm^3)
		x	y	z			
Middle frontal gyrus (lateral FPC)	R	32	48	16	10	0.0125	1,280
Middle frontal gyrus (lateral FPC)	L	−32	50	8	10	0.0124	680
Medial frontal gyrus (medial FPC)	L	−10	54	18	10	0.0113	600
Anterior cingulate	R	2	46	6	32	0.0107	584
Superior frontal gyrus (lateral FPC)	L	−34	50	22	10	0.0096	368
Precentral gyrus	L	−40	4	36	9	0.0079	320
Middle frontal gyrus	L	−54	10	36	9	0.0072	SC
Medial frontal gyrus (medial FPC)	L	−12	48	4	10	0.0077	176
Middle frontal gyrus	L	−50	2	42	6	0.0081	152
Superior parietal lobule	R	30	−56	52	7	0.0113	1,176
Inferior parietal lobule	R	36	−46	40	40	0.0095	SC
Inferior parietal lobule	L	−42	−46	46	40	0.0105	624
Precuneus	R	28	−70	38	19	0.0079	120
Cuneus	L	−28	−78	32	19	0.0104	280
Cuneus	R	18	−78	20	18	0.0077	152
Inferior temporal gyrus	R	40	−62	−2	37	0.0116	1,024
Fusiform gyrus	R	32	−58	−12	37	0.0105	SC
Thalamus	R	8	−10	6		0.0156	1,016
Lentiform nucleus	L	−12	−4	2		0.0110	320

Hem, hemisphere; BA, Brodmann area; ALE, activation likelihood estimation; FPC, frontopolar cortex; SC, same cluster.

lobules. The observation that a circumscribed set of regions (IFJ and PPC) from within the widespread fronto-parietal switching network were involved in all three forms of switching suggests that these regions contribute to cognitive processes common to attention shifting in a domain-general manner. Two cognitive processes which are thought to contribute to all forms of switching are representing and updating task sets [Miyake et al., 2000], making IFJ and PPC potential contributors to these domain-general switch processes.

If IFJ and PPC contribute to representing and updating task sets during task switching, then two expectations should follow. The first expectation is that there should be existing evidence supporting a role for IFJ and PPC in representing and updating task sets from previous studies. There is support for this expectation. Specifically, previous functional neuroimaging studies have suggested that IFJ appears to be involved in updating representations of task rules or sets across a range of cognitive control tasks [Brass and von Cramon, 2004; Derrfuss et al., 2004, 2005; Roth and Courtney, 2007; Roth et al., 2006, 2009]. Analogously, a body of evidence has demonstrated a role for PPC in representing task sets [Bunge et al., 2002, 2003; Cavina-Pratesi et al., 2006]. For example, PPC has shown sustained neural activity during a delay period before the stimulus presentation [Cavina-Pratesi et al., 2006] and has shown increased brain activity when comparing two stimulus-response alternatives with a single stimulus-response mapping [Bunge et al., 2003].

The intimate relationship between the cognitive processes of representing and updating task sets suggests a coordinated role of regions supporting these processes (i.e., IFJ and PPC). Thus, if IFJ and PPC contribute to the highly related cognitive processes of representing and updating task sets relevant to task switching, we would expect that task switching performance would be influenced by the strength of anatomical connectivity between these regions. There is support for this expectation. First, results from diffusion tensor imaging (DTI) tractography studies have demonstrated that portions of the IFJ (~BA 44/6) and PPC (~BA 40/7) are anatomically connected via the superior longitudinal fasciculus (SLF) [Catani et al., 2005; Makris et al., 2005]. Secondly, we recently found that the strength of anatomical connectivity (assessed via the DTI metric of fractional anisotropy) along the SLF tract is negatively correlated with switch cost RT in both young and older groups [Gold et al., 2010]. This finding suggests that faster task switching is associated with 'more direct' information flow between IFJ and PPC, in keeping with a view that these regions play a coordinated role during task switching.

Dorsal Premotor Cortex Shows Domain-Preferentiality for Perceptual Switching

Our meta-analyses found that pre-PMd was preferentially recruited for perceptual switching. The pre-PMd region comprises a rostral portion of premotor cortex (BA 6), which is situated anterior to motor cortex (M1; BA 4). However, pre-PMd is more heavily interconnected with PFC than M1 [Barbas and Pandya, 1987]. In accordance with this anatomical feature, recent evidence suggests that pre-PMd is involved in nonmotoric cognitive processes in addition to motor planning while caudal premotor cortex (i.e., premotor proper) is engaged in actual motor execution [Abe and Hanakawa, 2009]. Data from a body of lesion studies in the monkey and humans suggest that pre-PMd's role in stimulus-motor relationships relates to learning perceptually-driven, arbitrary stimulus associations as opposed to motor output [Abe et al., 2007; Amiez et al., 2006; Hanakawa et al., 2002; Hopfinger et al., 2000; Petrides, 2005]. Based on such evidence, an emerging theory is that pre-PMd is involved in learning and applying rule-based associations between perceptual features of stimuli and responses [Badre and D'Esposito, 2009].

The pre-PMd activation associated with perceptual switching was close (particularly in the left hemisphere) to the frontal eye fields (FEF; BA 8). The FEF have a well-established role in saccadic eye movements [Keating, 1991]. However, there is accumulating evidence that FEF are involved in attention and working memory processes beyond saccadic eye movements [Awh et al., 2006]. Of particular relevance, a recent study demonstrated that FEF activity persists when maintaining auditory-cued space, even for locations behind the head to which it is impossible to make saccades [Tark and Curtis, 2009]. These data suggest that FEF contributes to high-level working memory processes which broadly support spatial attention shifts, even in the absence of saccades.

However, it has been unclear from individual functional neuroimaging studies of task switching whether pre-PMd (or FEF) is involved in perceptual switching per se. There are likely several reasons for this knowledge gap. First, some functional neuroimaging studies used passive control conditions (i.e., fixation or rest) or control conditions which had perceptual and motor demands that were much simpler than those of the switching condition. Second, some studies reporting pre-PMd activation have utilized multidimensional perceptual-and-response switching tasks (such as the color/shape task), making it difficult to tease apart pre-PMd's contribution. Finally, pre-PMd activation in any one particular imaging study could be idiosyncratic to one group of subjects or switch task.

In the present meta-analyses, all contrasts compared conditions which required similar perceptual and motor requirements (i.e., switch vs. nonswitch trials but not switch vs. passive fixation or rest baselines). In addition, care was taken in the present meta-analysis to insure that perceptual switching studies did not include response switching. Finally, because our meta-analyses included multiple samples of participants, and multiple kinds of perceptual switching tasks, it is likely to be less affected by statistical idosyncrasies than individual studies. Thus, results from the present meta-analysis suggest that pre-

PMd (and possibly FEF) is actively involved in the switching processes in a domain-preferential manner: it appears to contribute to switching attention between perceptual features of stimuli (e.g., shape and direction) as opposed to switching between response mappings or contextual rules.

Frontopolar Cortex Shows Domain-Preferentiality for Context Switching

The present meta-analysis revealed that context switching preferentially activated lateral and medial regions of FPC (BA 10). The context switching studies classified here emphasized shifting between cognitive sets or rules. Unlike perceptual or response switches, context switches are not triggered by a direct cue-task association. Context switches thus emphasize endogenous control processes associated with the internal generation and maintenance of task sets [Dreher et al., 2002]. The present finding of preferential FPC activation during context switching is consistent with a body of work linking FPC with the internal generation of high-level cognitive representations. For example, FPC has been associated with planning [Koechlin et al., 1999, 2000; van den Heuvel et al., 2003] envisioning/predicting future events [Okuda et al., 2003; Partiot et al., 1995], reasoning [Christoff et al., 2001; Green et al., 2006; Kroger et al., 2002], maintaining rules guiding subsequent cognitive activity [Sakai and Passingham, 2006], and endogenous set switching [Rogers et al., 2000; Weidner et al., 2002].

In the present meta-analysis, FPC activation was specific to context switching. This region was not activated during perceptual switching or response switching (the latter is discussed below). The preferential response of FPC to context switching suggests that it, like pre-PMd, constitutes a region of the brain that is sensitive to the type of switch performed as opposed to IFJ and PPC, which appear to contribute to switching in a more domain-general manner. The dissociation between FPC and pre-PMd according to switch type demonstrates that switching is not controlled by a single set of brain regions. Instead, our results demonstrate that multiple brain regions are capable of guiding switches, with regional specialization depending upon the kind of switching being performed.

Dorsolateral Prefrontal Cortex Contributes to Both Response and Context Switching

Results from the direct comparison showed that DLPFC was activated most strongly by response switching. Also, results from individual ALE analyses found DLPFC activation during response switching but not perceptual switching. This finding is consistent with several recent studies which have directly contrasted perceptual-based and response-based cognitive control processes. For example, Ravizza and Carter [2008] found greater DLPFC activity for response switching than for perceptual switching and

greater pre-PMd activity for perceptual than response switching. Similarly, in our recent work using a modified version of the Stroop task, DLPFC was activated during response conflict but not perceptual conflict [Kim et al., 2010a; Kim et al., 2010b].

However, in the present meta-analyses, DLPFC recruitment was not specific to response switching. Instead, DLPFC was also activated during context switching. One possible reason for the activation DLPFC during both response and context switching, but not perceptual switching, is that the former two switch types likely place greater emphasis on the maintenance and manipulation of information within working memory, processes which have been linked with the DLPFC [e.g., D'Esposito et al., 1998, 1999]. A different possibility is that only specific portions of the DLPFC are preferential for response switching. For example, the peak DLPFC activation we observed for context switching was dorsal and anterior to that observed for response switching (see Figs. 2 and 3). These different possibilities should be contrasted in future studies which include both response and context switching tasks and explicitly manipulate levels of working memory within these tasks.

An Anterior-Posterior PFC Gradient Associated With Endogenous Switching Processes

Overall, the present results suggest an anterior-to-posterior gradient within PFC for task switching, according to the degree of endogenous control processes. The most anterior activations were observed for context switches, which are not triggered by a direct cue-task association. Context switches thus emphasize endogenous control processes associated with the internal generation and maintenance of task sets [Dreher et al., 2002]. In contrast, the most posterior activations were observed for perceptual switching. Perceptual switches can be viewed as relatively low in the need for endogenous control processes because they are driven by external cues that directly indicate the upcoming task [Logan and Bundesen, 2003]. Perceptual switches thus minimize the need for endogenous control processes because of the facilitative contribution of the cue to the retrieval and maintenance of task set [Koch, 2003]. The anterior-to-posterior task switching gradient we observed according to the level of endogenous control is consistent with evidence for a similar gradient across several other cognitive domains [Badre and D'Esposito, 2007].

The present meta-analysis had several caveats that highlight open questions and may help guide future research. First, as with all meta-analyses, results will need to be tested in functional neuroimaging studies that compare activation patterns of each switch type in the same group of participants. Second, our analyses were restricted to only three kinds of task switching. The switch types were chosen because they have been used frequently in the task switching literature. However, there are other forms of

task switching that were not explored in the present meta-analysis, some of which may be associated with different neural correlates than those reported here. For example, Wager et al. [2004] reported that the spatial distribution of peak activation clusters within the parietal lobe differs between location switching and object attribute switching. The fact that our meta-analyses did not explore attention shifts associated with spatial location may be one reason why no differences between switch types were observed in the parietal lobes.

CONCLUSION

The current meta-analysis provides evidence concerning the degrees of domain-preferentiality of frontoparietal brain regions during task switching. We found that IFJ and PPC were commonly activated by perceptual, response, and context switching tasks, suggesting that these regions contribute to domain-general task switching processes (such as task representation and updating). Results also indicated more domain-preferential roles for two PFC regions: pre-PMd was preferentially associated with perceptual switching, and FPC was preferentially associated with context switching. These findings suggest that switching is not controlled by a single set of brain regions. Instead, multiple brain regions appear to be capable of guiding task switches, depending upon the type of switch being performed. Consequently, our findings suggest that switching is not a unitary process and that future cognitive control studies employing task switching paradigms should consider the type of switch being performed. In addition, our results provide regions of interest that can be used in future functional neuroimaging studies to explore specific hypotheses about the functional neuroanatomy of task switching.

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