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Inhibit, switch, and update: A within-subject fMRI investigation of executive control

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ABSTRACT

An influential model of executive control suggests that it comprises three dissociable processes: working memory, inhibition, and task switching. Multiple studies have investigated how these processes are individually implemented in the human brain. However, few have directly investigated this question using a common task architecture and a within-subject design. Here, healthy adult humans (N = 22) performed a novel executive control task during fMRI scanning. The paradigm independently manipulated working memory updating, inhibition, and task switching demands, while keeping all other task features constant. Direct contrasts of each executive task with a closely matched control condition revealed a differentiated pattern of recruitment across control tasks: *working memory* was associated with activity in dorsolateral prefrontal, lateral parietal and insular cortices bilaterally; *Inhibition* engaged right lateral and superior medial prefrontal cortex, inferior parietal lobules bilaterally, right middle and inferior temporal cortex, and ventral visual processing regions; *Task switching* was associated with bilateral activity in medial prefrontal cortex, posterior cingulate cortex and precuneus, as well as left inferior parietal lobule, lateral temporal cortex and right thalamus. A conjunction of all executive versus control task activations revealed common areas of activation overlapping regions of canonical frontoparietal control and dorsal attention networks. Further, multivariate analyses suggest that working memory may be a putative common factor supporting executive functioning. Taken together, these results are consistent with a hybrid model of executive control in the human brain.

Higher-order cognition is an emergent property of interactions among a variety of component executive processes. This suggests that executive functioning can be conceptualized as a hybrid system with a superordinate control structure and fractionated, process-specific subsystems (Alvarez and Emory, 2006; Niendam et al., 2012; Zelazo et al., 1997). Several empirical and meta-analytic investigations have identified both overlapping and process-specific brain activations during executive control tasks (e.g. Collette et al., 2005; Derrfuss et al., 2004; McNab et al., 2008; Niendam et al., 2012; Turner and Spreng, 2012; Wager et al., 2004). An enduring model of executive functioning identifies three component processes (Miyake et al., 2000): (i) working memory - the ability to hold, manipulate and update information in mind, (ii) inhibition – the ability to withhold inappropriate responses and suppress irrelevant information, and (iii) task-shifting – mental flexibility, the ability to switch tasks or mental set. The neural bases of these executive processes have been extensively studied in isolation (e.g. *Working memory*: Jonides et al., 1997; *Inhibition*: Chambers et al., 2009; *Task-switching*: Kim et al., 2012). Few studies have used a within-subject experimental design to contrast brain activity between executive processes (e.g. Collette et al., 2005; Derrfuss et al., 2004; McNab et al., 2008; Swainson et al., 2003; Sylvester et al., 2003). Studies have typically investigated two, but not the three, central component processes simultaneously (but see Derrfuss et al., 2004 and Collette et al., 2005), and have used different task-paradigms for the different control processes. These studies report both overlapping and distinct brain activations across executive control tasks, with common areas of activation observed in the medial and lateral prefrontal cortex (PFC) as well as the superior and medial parietal cortices (e.g. Buchsbaum et al., 2005; Collette et al., 2005; McNab et al., 2008; Sylvester et al., 2003). Meta-analytic reviews of existing neuroimaging studies of executive

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control found support for both a superordinate executive control system, as well as process-specific patterns of brain activity (Niendam et al., 2012; Nowrangi et al., 2014; and see Turner and Spreng, 2012; Spreng et al., 2017 for similar reviews in the context of neurocognitive aging).

Taken together, these studies provide evidence for a hybrid model of executive functioning in the human brain (Niendam et al., 2012). The hybrid account involves both unified, or domain general, as well as diverse, or process-specific, areas of activity associated with the canonical executive functions. However, previous studies have used different paradigms (both task and control) to assay each executive function domain, leaving open alternative explanations for the hybrid (unity and diversity) account. Overlapping patterns of activation, evidence for the unity aspect of the hybrid model, may be attributable to domain general increases in working memory or contingent motor response demands as more complex rule structures are implemented for executive versus control tasks. Critically, relative differences in these (and likely many other) demands across highly variable task paradigms make it difficult to assess their contributions to the overlapping patterns of brain response observed in the hybrid account. On the diversity side of the equation, alternative explanations include relative differences between executive and control tasks across domains on processes of non-interest including visual, attentional or motor demands. Further, disparate task paradigms may introduce differences in task strategy unrelated to the executive functions of interest. As an example, dual (versus single) task performance in a task switching paradigm may promote strategies such as verbalization that are not as readily applied during anti- versus pro-saccade inhibition tasks.

Given these putative alternative accounts to the hybrid model posed by the use of disparate task paradigms, it is necessary to employ a matched task paradigm to fully interrogate the hybrid model of executive functioning. Here we developed a novel executive function paradigm with a matched task structure for each of the three executive control tasks (working memory, inhibition, task-switching). We adopted a layered task architecture, beginning with a common perceptual-motor control task, and adding a single rule to engage the executive control task of interest (see Fig. 1). By using this common task architecture, we are able to carefully calibrate, and thereby reduce, relative differences in working memory and contingent motor response demands (as two examples) across domains, in addition to rigorously controlling for visual perceptual and motor aspects of the tasks. This approach, while employing executive function tasks that are adapted from the rich literature in this field, enabled us to isolate and contrast brain activity associated with working memory updating, inhibition, and task switching more precisely.

We first investigated task-related differences in brain activity using univariate methods to directly contrast each executive control task with a perceptual-motor control. As executive control is increasingly considered to be an emergent property of functional interactions among distributed brain networks, we also used a multivariate approach, Partial Least Squares (PLS; Krishnan et al., 2011) to investigate whole-brain patterns of covariance among distributed brain regions over all three conditions simultaneously. We reasoned that if there was a spatially distributed, domain general executive control system, a common pattern of brain activity would emerge, distinguishing the three executive tasks from our closely-matched, visuomotor control. Consistent with the hybrid model (e.g. Collette et al., 2005; Niendam et al., 2012), we leveraged our executive control paradigm and within-subject experimental design to test our two central hypotheses: (i) Overlapping activation patterns across executive tasks would be spatially coherent with an executive control network, comprising dorsolateral prefrontal and parietal brain regions (unity hypothesis). (ii) Process-specific activation patterns would be identified for each executive function domain (diversity hypothesis). Process-specific activity would include regions of the left dorsolateral prefrontal cortex and inferior parietal lobule (working memory); right inferior frontal gyrus and pre-supplementary motor area (inhibition); and superior medial prefrontal cortex and posterior parietal cortex (task switching).

1. Materials and methods

1.1. Participants

Twenty-five healthy young adults were recruited into the study. Two participants failed to meet criteria on the practice task (66% accuracy) and were excluded. One participant was excluded from the analysis due to performing at chance on the experimental task while in the scanner. This left a final sample of 22 participants (11 women, 11 men, M_{age} = 22.14, age range: 18–28 years). Participants had no reported history of psychiatric or neurological illness. All procedures were approved by the Institutional Review Board of York University and the study was carried out in accordance with the Canadian Tri-Council's code of ethical conduct for research involving humans.

1.2. Experimental procedure

1.2.1. Experimental task

We created a paradigm to manipulate working memory, inhibition, and task switching while controlling for other task demands (e.g. motor, verbal, visual task features; see Fig. 1). During scanning participants were presented with three yellow and/or blue squares on a black background for each task trial and required to make a “yes” or “no” response. From this common task architecture, executive control conditions were created by layering rules, designed to engage specific executive processes, onto the baseline perceptual-motor control task. The experimental design included four conditions, described briefly below and presented in schematic form in Fig. 1.

1.2.2. Control task

In the baseline control condition, participants were instructed to simply attend to the perceptual features of the center square in the three-square array and respond to the question, “Is the middle square blue?”

1.2.3. Working memory updating task

The working memory task required participants to continuously update the contents of working memory. The stimulus array was identical to the control task and participants were now asked, “Was the middle square blue *two trials ago*?”

1.2.4. Inhibition task

During the inhibition condition, the participants carried out the baseline control task, answering “Is the middle square blue?” However, they were now asked to withhold their response if two (and only two) of the squares in the current array were yellow.

1.2.5. Task switching

To maximize the efficiency of the protocol, we leveraged task block changes to assess switching. A cue screen identifying each condition block (e.g., “2-back” for the working memory condition, “double yellow” for the inhibition condition) was presented for 1000 ms. The first trial of each task block following the cue was modeled as a task switch trial (Fig. 1). We designed this condition to capture neural activation related to the cognitive control processes associated with switching, independent from preparatory control and task-cue processing (i.e. “residual switch costs,” Monsell, 2003). Previous research has shown that task switching costs are associated with the first trial of a new task, even when cue-stimulus intervals are large (e.g. Altmann, 2006; Jost et al., 2013; Ruge et al., 2013; Schmitz and Voss, 2014) and switches are predictable (e.g. Dreher et al., 2002; Monsell et al., 2003; Tornay and Milán, 2001). These “residual switch costs” point to trial-wise cognitive mechanisms associated with switching, which are

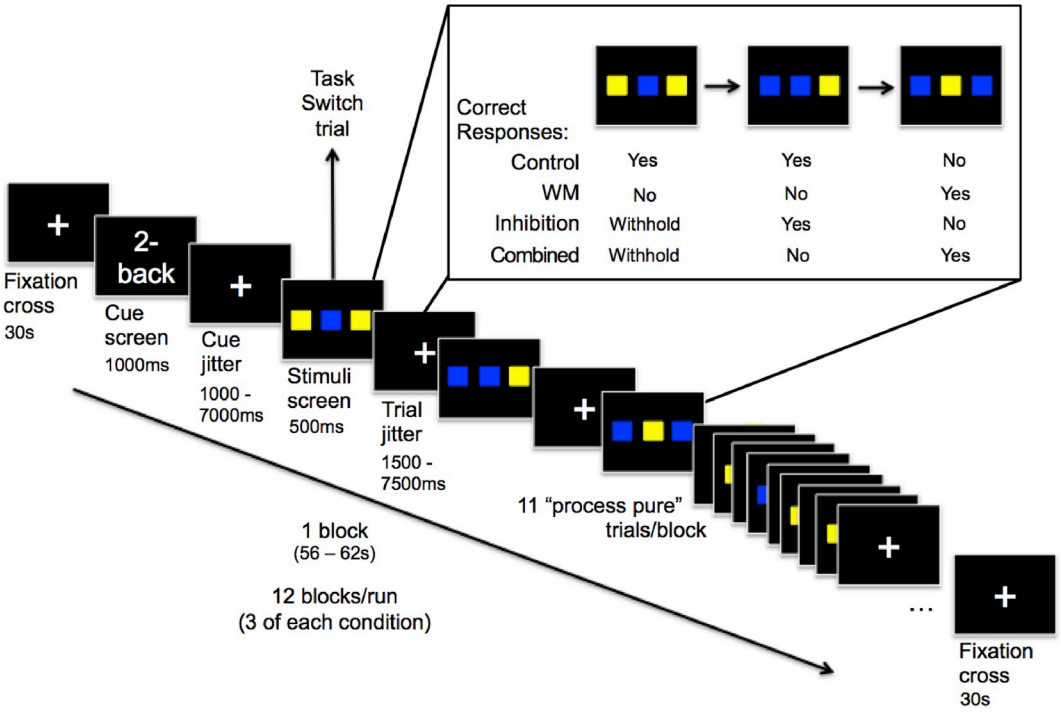

Fig. 1. Overview of the fMRI protocol. There were 12 trials/block: 1 task switch trial and 11 condition-specific or "process pure" trials. There were 12 blocks/run and 4 runs/session (3 blocks of each condition in a given run, and 12 blocks of each condition overall). A fixation cross was presented at the beginning and end of each run for 30 s. 1 run lasted 8 min and 48 s. The first trial of a new block was the Task Switch trial and came immediately after participants were given a cue to notify them which task is next. Inset panel: Overview of the different tasks used in the study. (i) Control "middle-blue" task: "Is the middle square blue?" (ii) Working Memory (WM) "2-Back" task: "Was the middle square blue two trials ago?" (iii) Inhibition "Double-Yellow" task: "Is the middle square blue? If two and only two squares are yellow, then do not answer." (iv) Combined Inhibition & Working Memory "Double-Yellow 2-Back" task: "Was the middle square blue two trials ago? If two and only two squares are currently yellow, do not answer." Responses underneath the images represent correct responses. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

separate from switch-cue processing and preparatory effects (for a review of these issues in the cognitive literature, see Monsell, 2003; and in the neuroimaging literature, see Ruge et al., 2013). Here we leverage our event-related design to isolate switching activity by having the onset of the 'switch' trial occur a minimum of 2000 ms after the cue, well outside the temporal range of the preparatory effect (about 600 ms after a cue is given, Monsell, 2003; Ruge et al., 2013). We also jittered the cue-stimulus interval, such that cue-related activity was modeled separately from the switch trial. This jittered paradigm, combined with the minimum latency between the cue and switch trials, allows us to isolate the neural effects of switching, consistent with previous research (e.g. Barber and Carter, 2005; Kimberg et al., 2000; Muhle-Karbe et al., 2014; Rushworth et al., 2002; Smith et al., 2004). See Supplementary Materials for extended account of the task switch condition.

1.2.6. *Working memory + inhibition*

Participants also completed a combined working memory and inhibition task. In this condition they responded whether the middle square was blue two trials ago, and were required to inhibit their response if there were two yellow squares in the current array. This condition does not assay the core canonical executive control processes and was included as part of a separate investigation examining parametric modulation of executive control demands. We report this condition in the full model analysis (Figs. 5, S1, S2) and the behavioral data (Table 1) for transparency. However, we do not discuss the combined condition further in this report.

1.2.7. *Overall structure of the experiment*

Participants completed a 30-min practice task, during which they familiarized themselves with the tasks and cues (control: "middle blue"; working memory: "2-back"; inhibition: "double yellow"; working memory & inhibition: "double yellow 2-back"). The experimental paradigm included 12 trials (1 task switch trial and 11 "process pure" trials) per block, 12 blocks per run (3 blocks of each of the 4 conditions listed above) and 4 runs per session. There were a total of 12 blocks of each condition throughout a scan session. This resulted in 132 working memory and inhibition trials (44 withhold) and 48 task switch trials. There was a 1:1 ratio of correct yes/no responses, and a 1:1:1 ratio of correct yes/no/withhold responses for the inhibition condition. The order of the blocks was pseudo-randomized for every participant, ensuring that the same condition was not presented back-to-back (to keep the task switch trials valid). Null trials, lasting between 2 and 6 s, were included to ensure sufficient jitter between events (Friston et al., 1999). Experimental runs were preceded and followed by 30 s of baseline rest, where the participants viewed a fixation cross. The experiment was presented using E-Prime 2.0 software (Psychology Software Tools,

Table 1
Mean accuracy and reaction times.

Condition	% Accuracy	Mean RT
Control	96.34 (0.03)	765.17 (139.71)
Working Memory	82.73 (0.15)	694.70 (185.16)
Inhibition	91.47 (0.05)	873.20 (150.51)
Inhibit trials	75.80 (0.14)	n/a (n/a)
Task Switching	89.96 (0.10)	947.40 (182.22)
Working Memory & Inhibition	70.25 (0.12)	939.40 (208.38)
Overall	85.96 (0.07)	810.04 (144.49)

Note. Mean (*SD*) of % accuracy and mean reaction time (in ms) for correct trials on each condition in the study, for all participants included in the analysis. The inhibition condition includes overall performance during the "double yellow" blocks, as well as performance on inhibit trials specifically, where the correct response was to withhold.

Pittsburgh, PA) and stimuli were viewed through a head-coil mounted mirror. All responses were made on a button box. 'Yes' or 'No' responses were recorded on every trial, with the exception of inhibition trials where participants withheld their responses. Participants were also instructed to answer 'No' on the first two trials of each working memory task block, as there were insufficient preceding trials to apply the 2-back rule.

2. MRI data acquisition and pre-processing

Participants were scanned using a Siemens 3T Magnetom Tim Trio MRI scanner with a 32-channel head coil. A T2*-weighted 2D EPI sequence sensitive to BOLD contrast was acquired in the oblique-axial plane (36 axial slices, 3 mm isotropic, TR = 2000 ms, TE = 30 ms, flip angle = 90°, field of view = 240 mm^2 with a 80 × 80 matrix size). High-resolution 3D structural images were acquired using a T1-weighted sequence, multi-planar rapid gradient echo (MP-RAGE) (192 slices, 1 mm isotropic, TR = 1900 ms, TE = 2.5 ms, TI = 900, flip angle = 9°, field of view = 256 mm^2).

For each of the 4 functional runs, 264 scans were collected. All pre-processing was accomplished using an in-house pre-processing pipeline based on Analysis of Functional Neuroimages software (AFNI: Cox, 1996). Physiological noise regressors were generated to regress out noise due to respiration and heart rate. Each volume was corrected for slice-time dependent offsets. Each participant's scans were then motion-corrected to the 8th volume of the first run of the session. A Freesurfer segmentation was used to calculate white matter and CSF masks on the T1-weighted image, which were then co-registered with the functional data (Fischl et al., 2002). Whole-brain masks were calculated on the mean of the functional data. Each voxel's time series was detrended against Legendre polynomials up to the 4^{th} order and a regression model including the 6 AFNI head motion parameters, the physiological (respiration and heart rate) regressors, as well as the mean and first lag of the ventricle, CSF, and a voxel-wise local white matter (15 mm) timeseries was fit to the data to account for physiological and scanner-induced sources of noise (ANATICOR: Jo et al., 2010). Residuals were carried forward to analysis. The data were smoothed within the whole-brain mask using a Gaussian kernel of full-width, half-maximum of 6 mm. Scans were transformed to the Montreal Neurological Institute (MNI) template.

2.1. Data analysis

2.1.1. Behavior

Behavioral data were analyzed in SPSS (IBM SPSS Statistics, Version 22.0, IBM Corp, Armonk, NY). We analyzed participants' accuracy (percent correct trials) and mean reaction times (RT) for correct trials for each condition using a one-way repeated-measures design. We used Shapiro-Wilk tests to assess whether there was evidence that the assumption of normality was violated in both the accuracy and RT data. Where there was evidence that the data were not normally distributed, non-parametric tests were implemented. We also ran Mauchly's test of sphericity on these data to assess whether carrying out a standard *F*-test was appropriate. Where we found evidence that our data did not meet the assumption of sphericity, we applied a Greenhouse-Geisser correction to our degrees of freedom when considering the statistical significance of the *F*-test. For fMRI analyses, correct responses were modeled for task switching and working memory updating, while successful withhold trials were modeled for the inhibition condition.

2.2. Neuroimaging

2.2.1. Univariate analysis

We first carried out a univariate, event-related analysis of the neuroimaging data using AFNI. Single-subject, multiple regression modeling was performed using the 3dDeconvolve program. Each condition of interest (control, working memory, inhibition, and task-switching trials) was modeled by convolving the hemodynamic response function with the onset and duration of the trial events using the gamma model. Additional events were modeled but not analyzed, such as the cue screen, the combined working memory and inhibition events, and non-withhold trials during the inhibition condition block. The single-subject beta-coefficients for each condition of interest from this contrast were then carried forward to a group-level, 2-factor, mixed-effects ANOVA, using the 3dAnova2 program. Statistical contrasts at the group level were computed for the control condition against each of the executive conditions of interest, creating 3 contrast images, one for each executive function. All analyses had conservative False Discovery Rates (all tasks $p < .01$), reducing the risk of type I error (Eklund et al., 2016).

For the univariate full model analysis, beta-coefficients from the three executive tasks were contrasted with those from the perceptual-motor control task, again in a group-level, 2-factor, mixed-effects ANOVA, using the 3dAnova2 program. As regional activations in the full model analysis could be biased by activity in a single task, we also conducted a conjunction analysis to directly investigate areas of activity common to all control processes. For the conjunction analysis, each task versus control contrast map was thresholded, inclusively masked, and multiplied to identify areas of overlap. Two common thresholds were applied to the contrast maps ($p < .01$ and $p < .05$) resulting in joint probabilities of 10^{-6} and 10^{-4} respectively for detecting common areas of activation across all three tasks (Cabeza et al., 2004).

2.2.2. Multivariate analysis

Spatiotemporal PLS is a multivariate functional neuroimaging analysis tool designed to identify whole brain patterns of activity that are correlated with tasks. PLS is a widely used analysis technique that is sensitive to distributed voxel response patterns, rather than the activity of individual voxels *per se* (Krishnan et al., 2011; McIntosh et al., 2004). PLS assesses the covariance between brain voxels (BOLD signal) and the experimental design to identify a limited number of orthogonal components (latent variables, LVs) that optimally relate the two. This data-driven approach identifies patterns of brain activity that covary with the experimental design and is well suited to identify common and dissociable patterns of brain activity across multiple task conditions. Our group has published extensively using these methods (e.g. Spreng et al., 2010; Spreng and Schacter, 2012; Turner and Spreng, 2015).

Activity at each time point, relative to trial onset, for each voxel is averaged across trials of a given condition and normalized to activity in the first TR of the trial and the data matrix is then expressed as voxel-by-voxel deviation from the grand mean across the entire experiment. This matrix is then analyzed with singular value decomposition to derive the optimal effects in the data. Here, we applied a PLS analysis to event-related fMRI data and the results provide a set of brain regions wherein activity is reliably related to the task conditions at 8 post-stimulus time points (i.e., 8 TRs = 16 s) for each LV. Each brain voxel is given a singular value weight, known as a salience, which is proportional to the covariance of activity with the task contrast at each time point on each LV. Multiplying the salience by the BOLD signal value in that voxel, and summing the product across all voxels, gives a brain score for each participant for each time point on a given LV. These scores can be used to examine differences in brain activity across conditions by comparing the 95% confidence intervals calculated from the bootstrap (see below), as greater activity in brain areas with positive (or negative) weights on a latent variable will yield positive (or negative) mean scores for a given condition over each time point.

The significance of each LV as a whole is determined by permutation testing, using 500 permutations. In a second, independent step, the reliability of the saliences for the brain voxels across subjects, characterizing each pattern identified by a LV, is determined by bootstrap resampling, using 300 iterations, to estimate the standard errors for each voxel. Clusters larger than 100 mm^3 comprising voxels with a ratio of the salience to the bootstrap standard error values (i.e., the

"bootstrap ratio"; BSR) greater than 2.5 ($p < .0124$) are reported. The local maximum for each cluster was defined as the voxel with a BSR higher than any other voxel within a 2 cm^3 centered on that voxel. PLS identifies whole brain patterns of activity in a single analytic step, thus, no correction for multiple comparisons is required. Although most brain regions showed reliable activations across multiple time points, results report the BSR for the second TR (i.e., 4 s post trial onset). In selecting this TR, we attempted to balance the typical timing of the hemodynamic response function's peak (4–6 s) with the potential contamination of subsequent trials (at 4 s, there is a maximum of only one intervening trial). Further, this lag time maximally differentiated the brain scores for the executive versus control task contrasts.

To test our main hypothesis of overlapping versus differentiated neural representations associated with executive control processing we conducted a single, full model PLS analysis. All executive conditions and the control condition were entered into this analysis, providing a critical, data-driven test for shared or dissociable neural activity patterns underlying the three executive control processes.

Additional control analyses confirming the validity of switch trial modeling and results can be found in Supplementary Materials.

3. Results

Accuracy (percent correct trials) and mean RT for correct trials for each condition are reported in Table 1. D-prime values were also calculated for the inhibition trials ($d' = 3.15$, $SD = .57$, range: 1.99–4.55). There was evidence that the assumption of normality was violated in the accuracy data, and a Friedman test was conducted to evaluate differences between participants' median accuracy for each condition. This test was significant ($\chi^2(4) = 59.99$, $p < .001$, Kendall coefficient of concordance = 0.68). Follow-up pairwise comparisons were conducted using Wilcoxon tests (with Bonferroni correction, $p = .005$). Performance on the control condition was significantly higher than all other conditions, while there were no differences in accuracy between working memory, inhibition, and task switching tasks. We examined the differences in mean RT using a one-way repeated-measures ANOVA. There was a significant effect of condition ($F(2.36, 49.58) = 25.83$, $p < .001$, $\eta^2 = .55$, after applying Greenhouse-Geisser correction for sphericity assumption violation). Follow-up pairwise comparisons revealed that RTs were significantly different across all conditions (at the corrected alpha value of .005) with the exception of control vs. working memory. RT differences for the three individual executive control conditions were as follows: working memory < inhibition response trials ($p < .001$), working memory < task switching ($p < .001$), inhibition < task switching ($p = .002$).

3.1. Neuroimaging results

No data were excluded during preprocessing due to participant motion, which was minimal. Framewise displacement values: $M = 0.08$, $SD = 0.01$, min = 0.06, max = 0.13.

3.1.1. Univariate analysis

Regional differences in brain activity, identified from group-level contrasts of each executive control task versus the control condition, are reported below (see Fig. 2 and Tables 2–4).

Working memory (contrast: working memory vs. control, Fig. 2A, Table 2) was associated with activation in lateral PFC and lateral parietal brain regions bilaterally, as well as middle temporal gyrus and subcortical regions ($t = 3.85$, $p < .001$, FDR: $q = .002$). *Inhibition* (contrast: inhibition vs. control, Fig. 2B, Table 3) was associated with activation in the right lateral and medial PFC, inferior parietal lobule bilaterally, lateral and inferior temporal cortex, and ventral visual processing regions ($t = 3.85$, $p < .001$, $q = .032$). *Task switching* (contrast: task switching vs. control, Fig. 2C, Table 4) was associated with activation in dorsolateral PFC regions bilaterally, cingulate cortex, superior medial frontal cortex, right precuneus, left lateral inferior parietal lobule, and lateral temporal lobes bilaterally ($t = 3.85$, $p < .001$, $q = .003$).

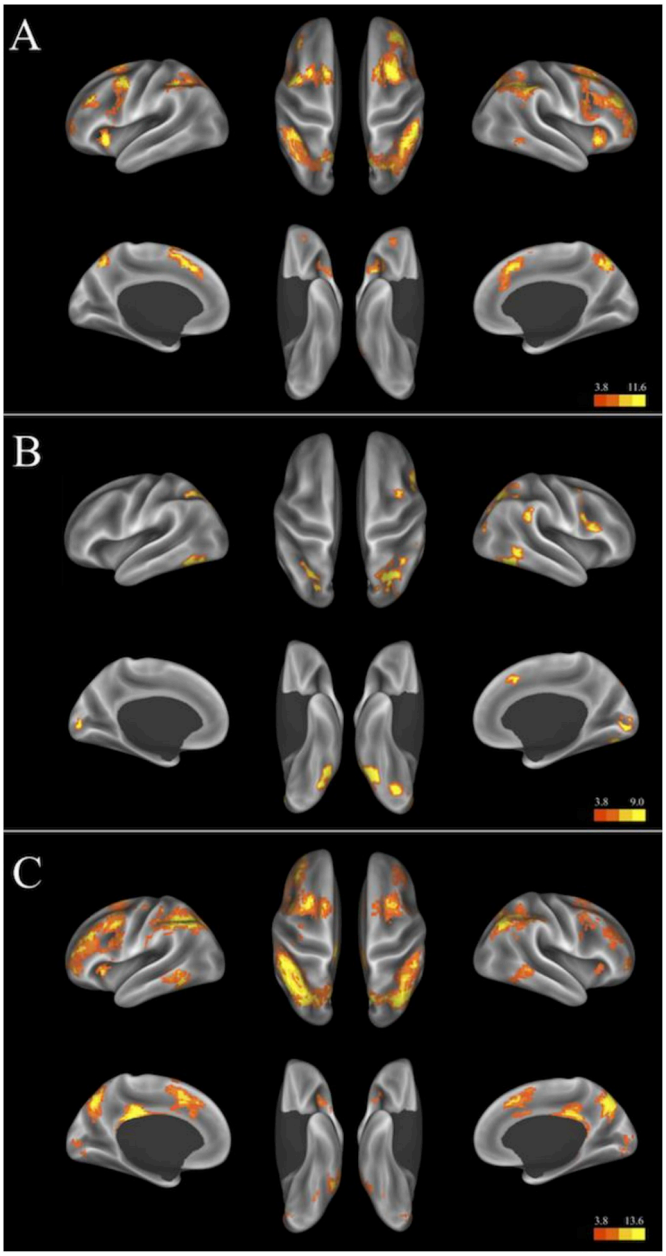

Fig. 2. Group-level brain activity for the three executive tasks versus the control task. Panel A: Working memory updating; Panel B: Inhibition; Panel C: Task switching. Images are projected onto partially inflated cortical surface maps using the connectome workbench visualization software. (http://www.humanconnectome.org/software/connectome-workbench.html). Left hemisphere is shown on the left, right hemisphere is shown on the right. Image thresholded at $p < .001$ ($t = 3.85$). Legend represents t-values.

A full model contrasting all executive tasks versus the perceptual-motor control condition revealed a spatially distributed pattern of activation including bilateral prefrontal cortex (lateral and medial aspects), left insula, bilateral parietal lobes, and right lateral temporal lobe, as well as subcortical regions including thalamic, basal ganglia, and cerebellar structures (Fig. 3, Table 5). A conjunction analysis showing direct overlap of activation across all three task v. control contrasts closely replicated the full contrast model. At a combined threshold of 10^{-4} (single contrast = $p < .05$), overlapping activations

Table 2
Brain regions associated with working memory.

Region	MNI Coordinates			Volume (voxels)	*t*-value
	X	Y	Z		
Frontal Lobe					
Right Middle Frontal Gyrus	33	3	54	3966	11.62
Right Middle Frontal Gyrus	33	3	54	292	11.62
Left Middle Frontal Gyrus	−48	3	45	401	8.61
Right Caudate	18	3	21	242	7.83
Right Superior Frontal Gyrus	36	36	30	242	8.28
Right Middle Frontal Gyrus	30	45	9	134	7.49
Left Insula	−30	21	3	50	8.23
Left Superior Frontal Gyrus	−36	57	15	188	6.26
Left Lentiform Nucleus	−12	0	3	496	8.75
Parietal Lobe					
Right Inferior Parietal Lobule	51	−39	45	1731	10.37
Right Inferior Parietal Lobule	51	−39	45	498	10.37
Left Inferior Parietal Lobule	−42	−48	51	211	8.87
Temporal Lobe					
Right Middle Temporal Gyrus	57	−54	9	22	5.46
Hindbrain					
Left Cerebellum	−33	−66	−27	257	7.30
Right Cerebellum	39	−60	−30	161	6.74

Note. Results from the univariate analysis contrasting working memory trials against control trials. Minimum cluster size: 20 adjacent voxels. Original cluster maxima reported (aligned left), as well as sub-maxima (indented, italicized) for larger clusters (> 500 voxels). Sub-maxima were identified by applying an increasingly stringent threshold until clusters with < 500 voxels emerged. MNI coordinates and *t*-values are reported for all cluster maxima and sub-maxima.

Table 3
Brain Regions associated with Inhibition.

Region	MNI Coordinates			Volume (voxels)	*t*-value
	X	Y	Z		
Frontal Lobe					
Right Inferior Frontal Gyrus	51	12	24	59	6.12
Right Middle Frontal Gyrus	33	0	42	25	4.82
Right Medial Frontal Gyrus	9	24	45	21	5.75
Parietal Lobe					
Left Inferior Parietal Lobule	−24	−63	48	59	5.65
Right Inferior Parietal Lobule	57	−42	27	27	6.25
Temporal Lobe					
Right Middle Temporal Gyrus	30	−57	33	249	6.02
Right Inferior Temporal Gyrus	45	−54	−9	88	8.12
Occipital Lobe					
Left Inferior Occipital Gyrus	−42	−69	−12	49	6.44
Right Cuneus	9	−87	3	75	5.88
Right Lingual Gyrus	21	−75	−6	34	6.49

Note: Results from the univariate analysis contrasting all inhibition withhold trials against control trials. MNI coordinates and *t*-values are reported for all cluster maxima. Clustering notes as per Table 2.

were observed in lateral frontoparietal, medial prefrontal, insular, and lateral temporal regions. This pattern became right lateralized at the combined 10^{-6} (single task = $p < .01$) threshold (Fig. 4 A-B, Table 6).

3.1.2. Multivariate analysis

When all conditions were entered into a single multivariate analysis model without specified a priori contrasts to test our overlap versus differentiated hypothesis, two significant latent variables (LVs) emerged. The first LV ($p < .001$) accounted for 82.45% of the covariance in the data and dissociated task switching from all other, non-switch task conditions (see Fig. 5A). The pattern of brain activity associated with task switching included the precuneus and the left superior parietal lobe, as well as the left middle frontal gyrus/dorsolateral PFC. This pattern also included the posterior cingulate gyrus and superior medial PFC (encompassing the supplementary motor area [SMA] and pre-SMA), as well as primary visual cortices (see Fig. 5B; Supplementary Table 1).

Table 4
Brain Regions associated with Task Switching.

Region	MNI Coordinates			Volume (voxels)	*t*-value
	X	Y	Z		
Frontal Lobe					
Right Middle Frontal Gyrus	36	51	0	86	7.22
Left Cingulate Gyrus	−3	−33	45	5574	9.98
Left Cingulate Gyrus	−3	−33	45	498	9.98
Right Medial Frontal Gyrus	3	18	48	117	9.03
Left Middle Frontal Gyrus	−33	0	45	57	9.45
Left Middle Frontal Gyrus	−42	30	33	49	8.98
Left Superior Frontal Gyrus	−30	0	60	45	9.73
Left Middle Frontal Gyrus	−41	44	17	35	8.5
Right Middle Frontal Gyrus	28	9	51	43	7.68
Left Insula	−48	15	0	20	4.89
Parietal Lobe					
Right Precuneus	9	−66	45	3063	13.66
Right Precuneus	9	−66	45	367	8.47
Right Precuneus	36	−69	45	306	10.98
Left Inferior Parietal Lobule	−45	−42	48	367	10.57
Right Thalamus	9	−12	15	499	8.47
Temporal Lobe					
Left Middle Temporal Gyrus	−51	−39	−9	1834	10.01
Left Middle Temporal Gyrus	−51	−39	−9	196	10.01
Right Middle Temporal Gyrus	63	−42	−3	156	8.37

Note: Results from the univariate analysis contrasting switch trials against control trials. MNI coordinates and *t*-values are reported for all cluster maxima and sub-maxima. Sub-maxima and clustering notes as per Table 2.

A second significant LV ($p = .012$) accounted for 11.51% of the covariance in the data and reflected a dissociation of the inhibition condition from all other conditions (see Fig. 5C). Left motor cortex activity was associated with the non-inhibition conditions, consistent with a right-handed button press. Areas positively associated with the inhibition trials included the bilateral anterior inferior and middle frontal gyri, as well as the superior medial frontal gyrus, proximal to pre-SMA (see Fig. 5D, Supplementary Table 2).

Notably, we did not observe a pattern related to level of executive control demand (i.e. dissociating the control task from the executive tasks). Nor did we observe a pattern of brain activity dissociating working memory from the other executive control conditions. Extended results examining the switch condition are in Supplementary Materials. We discuss the possible interpretations of these multivariate results in more detail below.

4. Discussion

We used a common task architecture and a within subject experimental design to investigate differences in how three canonical executive control processes are represented in the human brain. Individual task versus control contrasts revealed expected patterns of brain activity for working memory updating, inhibition, and task switching (see Niendam et al., 2012 for a meta-analytical review). A three-way conjunction of these contrasts revealed that the executive control tasks recruited a common set of regions closely overlapping the canonical dorsal attention system and frontoparietal control systems (e.g. Corbetta et al., 2008; Vincent et al., 2008). An exploratory, data-driven, multivariate analysis failed to reveal a common pattern of brain activity dissociating executive tasks from the control condition, which would imply the absence of a unitary executive system. However, the pattern of multivariate findings may also suggest that working memory might represent a common factor underlying executive functioning. These findings are discussed in further detail below.

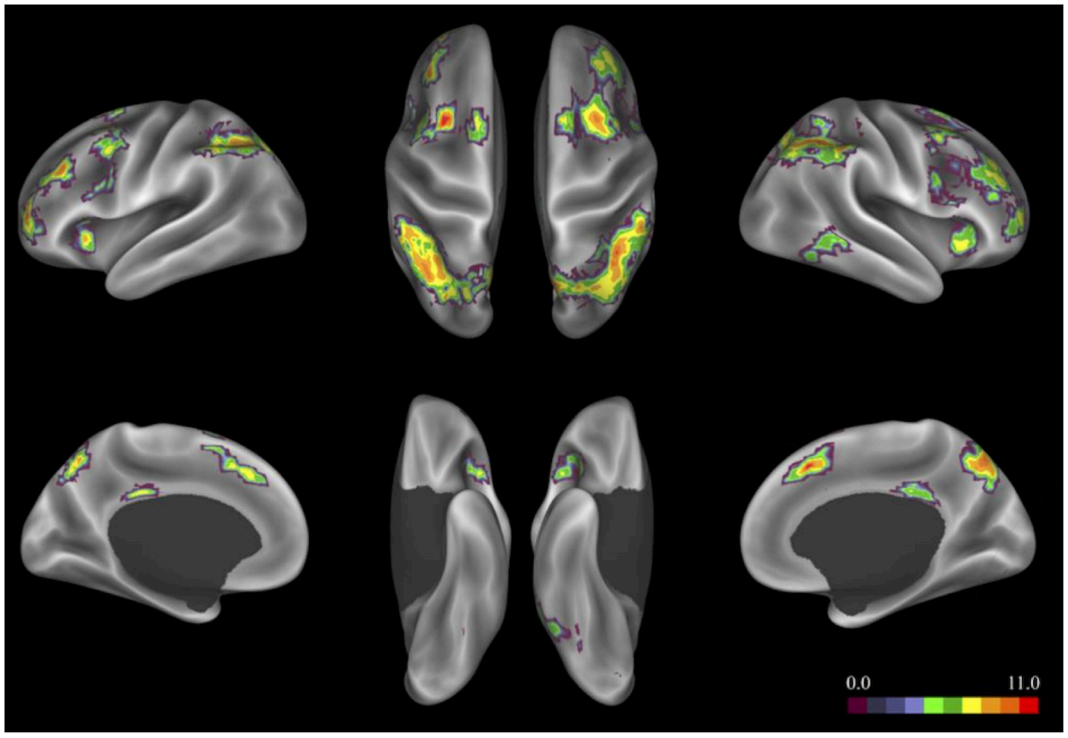

Fig. 3. Univariate full model contrast. Group-level contrast of the three executive control processes (working memory updating, inhibition, task switching) versus the perceptual-motor control task. Legend represents *t*-values. Left hemisphere is shown on the left, right hemisphere is shown on the right.

Table 5
Coordinates for the Three Executive Conditions vs. Control Univariate Contrast.

Region	MNI Coordinates			Volume (voxels)	*t*-value
	X	Y	Z		
Frontal Lobe					
Right Middle Frontal Gyrus	33	6	51	638	10.25
Right Middle Frontal Gyrus	33	6	51	302	10.25
Right Middle Frontal Gyrus	42	27	33	314	7.97
Right Middle Frontal Gyrus	33	57	6	124	7.27
Left Middle Frontal Gyrus	−36	57	12	174	10.03
Left Middle Frontal Gyrus	−39	27	36	102	8.15
Right Medial Frontal Gyrus	6	24	45	490	11.08
Right Lentiform Nucleus	21	18	0	801	8.42
Right Lentiform Nucleus	21	18	0	482	8.42
Left Insula	−30	24	3	92	7.97
Parietal Lobe					
Right Precuneus	9	−69	51	1409	10.36
Right Precuneus	9	−69	51	499	10.36
Right Inferior Parietal Lobule	39	−48	45	131	10.02
Left Inferior Parietal Lobule	−36	−60	45	177	9.31
Temporal Lobe					
Right Middle Temporal Gyrus	60	−48	−6	75	7.05
Hindbrain					
Left Cerebellum	−27	−72	−24	208	8.14
Right Cerebellum	6	−48	−18	37	8.04
Right Cerebellum	39	−57	−27	98	7.70

Note: Results from the univariate analysis contrasting all three executive conditions against the control condition. MNI coordinates and *t*-values are reported for all cluster maxima and sub-maxima. Sub-maxima and clustering notes as per Table 2.

4.1. Univariate analysis

A strength of our within-subject task design was that we were able to isolate brain activity associated with executive control processes of interest by contrasting these conditions against a closely matched control task. The resulting brain images revealed patterns of brain activity for working memory, inhibition, and task switching that were consistent with previous literature providing support for the construct validity of our novel paradigm.

Working memory. Brain regions showing greater working memory than control task activation included lateral PFC and lateral parietal brain regions bilaterally, as well as the middle temporal gyrus and subcortical regions (see Table 2, Fig. 2A). Activation of frontoparietal brain regions is consistent with previous N-back task studies (see Owen et al., 2005 for a review). The pattern of activation associated with working memory also mapped onto regions of the frontoparietal control network as defined by intrinsic functional connectivity analyses (Spreng et al., 2013; Vincent et al., 2008; Yeo et al., 2011).

Inhibition. Inhibition-related activity was observed in the right lateral and medial PFC, inferior parietal lobule bilaterally, lateral and inferior temporal cortex, and ventral visual processing regions (Table 3, Fig. 2B). These findings closely replicate those reported in a meta-analysis of studies examining brain activity during Go/No-Go tasks (Buchsbaum et al., 2005). They are also consistent with past reports demonstrating that right inferior frontal gyrus activity is associated with tasks requiring the suppression of a proponent response (e.g. Garavan et al., 1999; Konishi et al., 1999; Rubia et al., 2003; for review, see Aron et al., 2004). However, the neural correlates of inhibition extend beyond the right inferior frontal gyrus (Swick et al., 2011; Swick and Chatham, 2014). Right pre-SMA/SMA is also commonly associated with inhibition tasks (e.g. Chambers et al., 2009; Mostofsky and Simmonds, 2008; Simmonds et al., 2008). In addition to common regions of inhibition-related activation, we found activity in the primary visual areas, as well as the ventral visual pathway. We speculate that this ventral visual stream activity may reflect increased salience of the double-yellow visual cue in the inhibition task.

Task switching. Task switching-related activity was widely distributed, with clusters of activation observed in dorsolateral PFC regions bilaterally, precuneus, cingulate cortex, superior medial frontal cortex, right precuneus, left lateral inferior parietal lobule, lateral temporal lobes bilaterally, and right thalamus (see Table 4, Fig. 2C). These findings are consistent with neuroimaging studies of task

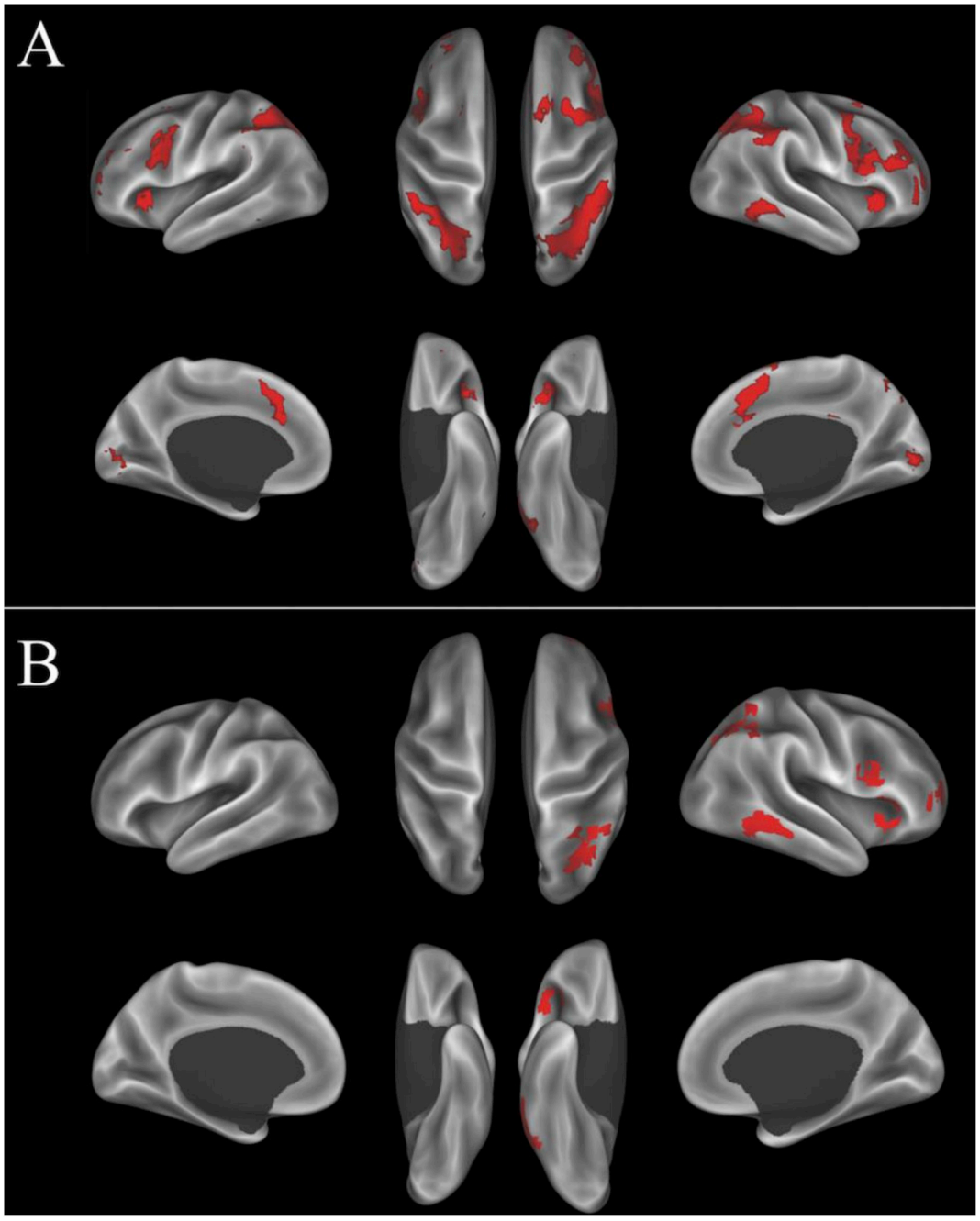

Fig. 4. Conjunction map of the three executive processes of interest. Red areas represent overlap among all three executive tasks versus the perceptual-motor control task, thresholded at $p < .05$ (joint probability of 10^{-4}, Panel A) and $p < .01$ (joint probability of 10^{-6}, Panel B). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 6
Brain Regions common to Working Memory, Inhibition, and Task Switching.

Region	MNI Coordinates			Volume (voxels)
	X	Y	Z	
Right Insula	40	23	3	34
Right Inferior Frontal Gyrus	47	12	24	26
Right Middle Frontal Gyrus	34	52	10	30
Right Inferior Parietal Lobule	37	−57	49	150
Right Middle Temporal Gyrus	58	−48	−9	55

switching, which implicate lateral PFC and superior/posterior parietal regions (Braver et al., 2003; Buchsbaum et al., 2005; DiGirolamo et al., 2001; Dove et al., 2000; Dreher et al., 2002; Jiang et al., 2018; Kim et al., 2012; Kimberg et al., 2000; Ravizza and Carter, 2008; Sohn et al., 2000; Wager et al., 2004). We observed a predominantly frontoparietal and left-lateralized pattern of brain activity during task switching relative to the perceptual-motor control task. Previous findings have suggested that switching requires both the maintenance of task-set as well as the semantic classification of the tasks as switching occurs (Braver et al., 2003; Kim et al., 2012; Ruge et al., 2013). This is consistent with our observation of overlap between working memory- and

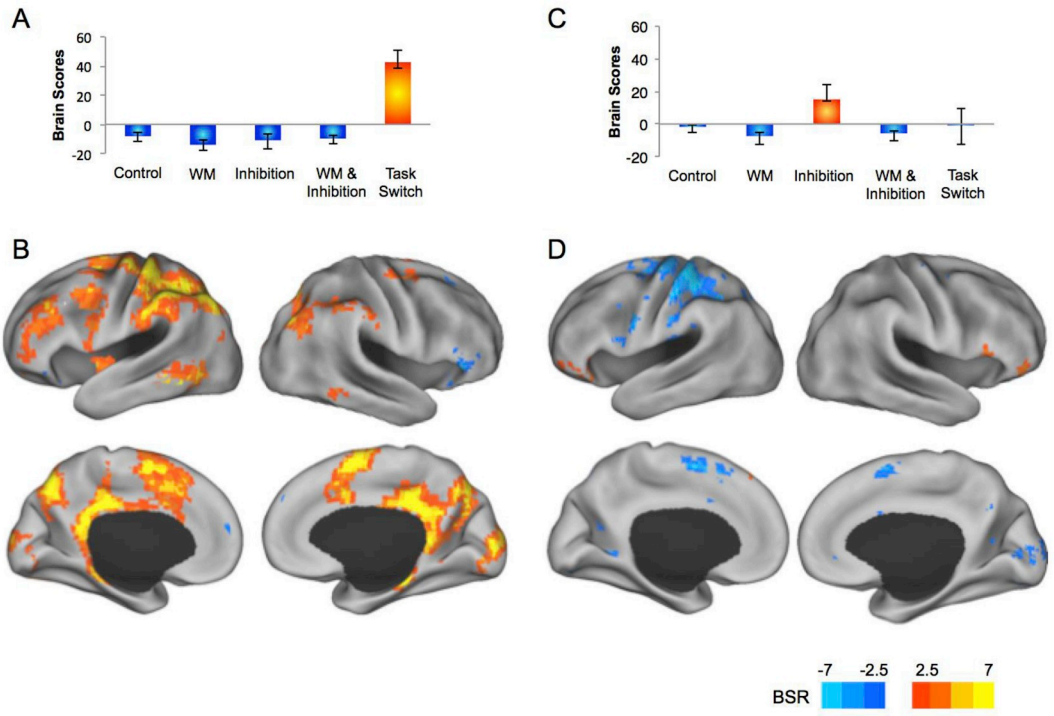

Fig. 5. Patterns of brain activity from the full model PLS analysis, where all conditions were included. WM = working memory. (A) Brain Scores for the first pattern of activity, dissociating task switching from all other conditions. Error bars represent 95% confidence intervals determined by bootstrapping analysis. (B) Whole-brain pattern of activity associated with task switching (warm colors) and all other conditions (cool colors). Data are displayed on the lateral (top row) and medial (bottom row) surfaces of the left and right hemispheres of a partially inflated surface map using CARET software (Van Essen et al., 2001). These brain images were generated using a BSR threshold of ± 2.5 ($p < .0124$), minimum cluster size of 20 voxels and minimum distance between clusters of 20 voxels. (C) Brain Scores for the second pattern of activity, dissociating inhibition from all other conditions. Error bars represent 95% confidence intervals determined by bootstrapping analysis. (D) Whole-brain pattern of activity associated with inhibition (warm colors) and the other conditions (cool colors). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

task switching-related activity in dorsolateral PFC bilaterally. This pattern of activation is generally consistent with our predictions based on past research, however the widespread pattern of activation observed here may also reflect engagement of other cognitive processes during the task switch trials. While speculative, these include task initiation necessary to engage the new rule set. Initiation has been associated with superior medial prefrontal regions reported here (Stuss et al., 2005). Activation of default network brain regions during the switch trials, while unpredicted, may reflect the shift from internal to external attentional systems as internal representations of rule set must be activated prior to the perceptual processing of stimuli at the first (switch) trial of each task block (e.g. Kucyi et al., 2016).

The novel executive paradigm implemented in this study modeled task switching as the first trial of each new block. As described above, this captured the residual switch costs associated with the shifting of rule sets across the blocks. While this approach was adopted to optimize the scan protocol in this study, it differs from other task switch paradigms reported in the literature. In Supplementary Materials we provide additional analyses to rule out alternative interpretations of these results and compare our findings with previous investigations of task switching. These results (see Figs. S1–S4) provide compelling evidence that our task switch condition is associated with a unique pattern of covariance that closely replicates patterns of brain activation associated with traditional assays of task switching.

To investigate whether all three canonical executive control processes recruited common brain regions we conducted two further analyses. First, we contrasted the three executive control tasks together against the perceptual-motor control condition (see Fig. 3). This analysis revealed a spatially distributed pattern of activation including bilateral prefrontal and parietal cortices cortex, lateral temporal lobes, and subcortical regions (Fig. 3, Table 5). This analysis replicates the meta-analytic findings reported by Niendam and colleagues (2012, see their Fig. 1), providing converging evidence that performance across variable executive control tasks engages a common substrate of brain regions, which closely overlap with the frontoparietal control network (Vincent et al., 2008). Recognizing that this full model contrast may reflect over- or under-representation of any one executive control task, we next conducted a conjunction analysis of all three executive functions versus control contrasts. This approach has the advantage of imposing a common statistical threshold across each contrast prior to entering the resulting maps into the conjunction (Cabeza et al., 2004), arguably providing the truest representation of activation overlap across the three tasks. As conjunction analyses are exquisitely sensitive to the thresholding imposed on each included contrast, we report both a standard ($p < .05$) and a more stringent statistical criteria ($p < .01$) for each contrast. Interestingly, at the more stringent statistical threshold, the overlap pattern becomes right lateralized (Fig. 4 A-B, Table 6). This pattern of activation, overlapping with dorsal attention network regions (Corbetta et al., 2008), highlights the importance of external attentional processes in the implementation of executive control in the human brain.

5. Multivariate analyses

In a final exploratory, multivariate approach we examined whether a pattern of distributed brain activity, dissociating executive control functions from the perceptual-motor control condition, would emerge from a data-driven, mode-free analysis. Specifically, we analyzed all conditions in a single model to determine whether a single activation pattern (i.e. a reliable latent variable in PLS) would emerge dissociating

all executive tasks from the control task. This multivariate analysis extended the univariate findings in two respects. First, as the approach is data-driven, the results are not constrained by a priori contrasts, providing a model-free test of the univariate findings. Second, this approach reveals whole-brain patterns of covarying activation, reflecting current perspectives on executive control as an emergent property of interactions among distributed brain regions (e.g. Dosenbach et al., 2007; Power et al., 2011; Vincent et al., 2008).

In contrast to predictions, this analysis failed to reveal a common pattern of brain activity dissociating the executive tasks from the control condition. Critically however, two significant patterns emerged. The first dissociated task switching from all other conditions (Fig. 5 A-B, Supplementary Table 1). This pattern closely reflected our univariate contrast (see Fig. 2, Panel C). Task switching-related activity was observed in the superior parietal lobule bilaterally, medial and lateral PFC (including the inferior frontal junction), consistent with previous meta-analytic reviews of task switching (e.g., Derrfuss et al., 2005; Kim et al., 2012; Wager et al., 2004). The second significant latent variable was associated with a pattern of brain activity that differentiated inhibition from all other conditions (Fig. 5 C-D, Supplementary Table 2). Consistent with our individual, univariate contrast and previous reports, inhibition-related activity was observed in right inferior frontal gyrus and pre-SMA (for reviews, see: Aron, 2007; Chambers et al., 2009; Mostofsky and Simmonds, 2008).

No pattern emerged from the full model analyses dissociating (i) working memory from the other tasks or (ii) all executive tasks from the control task. This presents two possible alternatives with respect to how our findings align with the fractionated versus hybrid accounts of executive control in the human brain. While speculative, we discuss these implications briefly here.

With regard to the absence of a 'working memory' LV, this may be due to the fact that all tasks, including the control task, shared common working memory demands. This could have precluded the emergence of a task-specific working memory LV, given the common working memory load associated with keeping the rules of the current task in mind. If this were the case, we might predict that reducing rule maintenance demands across all conditions (e.g. by including a task-cue on screen) would allow a distinct working memory task LV to emerge *dissociating brain activity associated with working memory updating from all others*. Such a result would be consistent with a fully-fractionated model of executive functioning, as each canonical process would have emerged as a distinct covariance pattern in this full model, multivariate analysis. Alternatively, if working memory represents a unitary factor underlying all executive control processes, then reducing the working memory load across tasks (again by including a task cue on screen) would result in a third LV dissociating *all executive tasks from the control task*, consistent with a hybrid account of executive control.

While we are unable to test these hypotheses directly here, the results of our univariate conjunction analysis, demonstrating close alignment with classic working memory activation patterns, provide some support for the latter interpretation (Fig. 4 A-B, Table 6). Although our findings are not definitive on this point, we suggest that working memory (Baddeley, 2003) may represent a unitary or common feature within an otherwise fractionated model of executive control processing, consistent with a hybrid account (Niendam et al., 2012).

6. Working memory as a common feature of executive control

The pattern of activation associated with working memory versus the control condition overlapped with elements of the 'executive network' identified in a meta-analytic review of brain activity during executive control (Niendam et al., 2012), and closely replicated our univariate full model and conjunction results at the lower threshold (Fig. 3; Fig. 4, panel A). At the higher statistical threshold, the pattern overlapped with both the canonical frontoparietal control and dorsal attention networks (Vincent et al., 2008, Fig. 4, panel B, Table 6). While speculative, this overlapping pattern of activation involving regions of the dorsal attention and executive control networks suggests that working memory may represent a common cognitive substrate supporting executive functioning. While the subject of ongoing research in our laboratory, we posit that these facets of executive control may be supported by aspects of these two canonical brain networks and their interaction in support of goal-directed cognition.

If confirmed, this conclusion would support a proposal associating executive, or goal-directed, control with activation in a frontoparietal multiple domain network (Duncan, 2010). In this model, executive control is conceptualized as sequential mental programming, requiring construction, maintenance, and context-specific reorganization of mental contents necessary to guide goal-directed behavior. While these processes clearly map onto the three control processes investigated here, our findings implicate working memory as a possible core driver of the multi-domain control system. This interpretation is in line with previous work establishing working memory as the only executive function significantly correlated with measures of general intelligence (Friedman et al., 2006). However, our current conclusion diverges from models of executive functioning which posit that task-switching (Dajani and Uddin, 2015) or inhibition (Miyake and Friedman, 2012), and not working memory as we suggest here, may be a common process supporting executive functions. This highlights the value of our approach in developing a novel, matched task design. Here we were able to carefully calibrate and match cognitive control demands across the three tasks by layering a single rule for each executive task onto the control task. Combined with our data-driven, multivariate analysis approach, we provide evidence that working memory demands, when carefully matched across tasks, may represent a unifying feature of executive functioning.

7. Limitations and future directions

Previous studies have used different tasks and control paradigms to identify overlapping and divergent patterns of brain activity associated with working memory, inhibition, and task switching (e.g. Collette et al., 2005; Niendam et al., 2012 for a review). Here we adopted a novel approach, developing a new paradigm to assay each of these domains within a single task architecture. While this approach allowed us to more precisely control for factors of non-interest and address alternative explanations for earlier findings, the tasks employed were adaptations of standard executive function paradigms. We believe the findings provide strong evidence supporting the construct validity of the tasks. However, future research will be necessary to confirm psychometric properties of these tasks. While a comprehensive validation of the tasks is beyond the scope of this investigation, work to better characterize their psychometric properties is underway in our laboratory.

Additionally, the task protocol here used a three-item array, and a one-rule manipulation of executive control. Future studies using a larger array size may provide more reliable and robust estimates of brain activity associated with these executive function processes. Follow-up studies using this paradigm may also introduce a task cue that remains on screen throughout the experiment to reduce overall working memory demands, making it more likely to identify a pattern of brain activity that dissociates the control task from the executive tasks in a multivariate analysis. Nonetheless, the single task architecture used in the current study allows for parametric manipulation of executive control by layering multiple rules onto the control task. This parametric manipulation may provide important insights into how the common executive control network identified by ourselves and others is engaged by increasing, and precisely calibrating, executive control demands. As noted above, we have designed a combined working memory and inhibition task condition (i.e. a two-rule manipulation) to explore this question.

Finally, a core motivation for this work was our earlier meta-

analytic reviews of how the neural basis of executive control is altered over the course of adult human development (Turner and Spreng, 2012; Spreng et al., 2017). As with any meta-analytic review, the findings are dependent on the often diverse task paradigms reported in the literature. An important future direction will be to investigate executive control and neurocognitive aging using the single task architecture implemented here.

8. Conclusion

Consistent with a meta-analysis of executive control (Niendam et al., 2012) and earlier empirical research (Collette et al., 2005; Derrfuss et al., 2004), our data provide support for a hybrid executive control system, involving a common frontoparietal working memory system and context-specific recruitment of sub-systems implicated in other control processes including inhibition and task-switching. These findings advance our understanding of the neural basis of executive functioning and provide novel insights into the unity and diversity hypotheses of executive control in the human brain.

Conflicts of interest

The authors declare no competing financial interests.

CRediT authorship contribution statement

Sabrina Lemire-Rodger: Conceptualization, Formal analysis, Visualization, Writing - original draft, Writing - review & editing. **Jaeger Lam:** Formal analysis, Data curation, Visualization. **Joseph D. Viviano:** Data curation, Formal analysis. **W. Dale Stevens:** Conceptualization, Supervision. **R. Nathan Spreng:** Formal analysis, Writing - review & editing, Supervision. **Gary R. Turner:** Conceptualization, Formal analysis, Writing - review & editing, Supervision.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2019.107134.

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