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Meta-analytic evidence for a superordinate cognitive control network subserving diverse executive functions

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Abstract Classic cognitive theory conceptualizes executive functions as involving multiple specific domains, including initiation, inhibition, working memory, flexibility, planning, and vigilance. Lesion and neuroimaging experiments over the past two decades have suggested that both common and unique processes contribute to executive functions during higher cognition. It has been suggested that a superordinate fronto–cingulo–parietal network supporting cognitive control may also underlie a range of distinct executive functions. To test this hypothesis in the largest sample to date, we used quantitative meta-analytic methods to analyze 193 functional neuroimaging studies of 2,832 healthy individuals, ages 18–60, in which performance on executive function measures was contrasted with an active control condition. A common pattern of activation was observed in the prefrontal, dorsal anterior cingulate, and parietal cortices across executive function domains, supporting the idea that executive functions are supported by a superordinate cognitive control network. However, domain-specific analyses showed some variation in the recruitment of anterior prefrontal cortex, anterior and midcingulate regions, and unique subcortical regions such as the basal ganglia and cerebellum. These results are consistent with the existence of a superordinate cognitive control network in the brain, involving dorsolateral prefrontal, anterior cingulate, and parietal cortices, that supports a broad range of executive functions.

Keywords Cognitive control · Prefrontal cortex · Executive function · Activation likelihood estimation · Meta-analysis

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Early cognitive theories posited that cognitive functions are modular in nature and located within separable but interconnected parts of the brain (Luria, 1970; Shallice, 1988). Within this framework, executive functions have been described as a set of superordinate processes that guide thought and behavior and allow purposive action toward a goal (Miller, 2000). These functions are critical for normal day-to-day cognitive functioning and appear to be particularly susceptible to altered development, injury, and disease. From a traditional cognitive or neuropsychological perspective, executive functions have been thought to comprise a set of distinct cognitive domains that include *vigilance*, or sustained attention (Pennington & Ozonoff, 1996; Smith & Jonides, 1999); *initiation* of complex goal-directed behaviors (Lezak, 1995); *inhibition* of prepotent but incorrect responses (Luna, Padmanabhan, & O'Hearn, 2010; Smith & Jonides, 1999); *flexibility* to shift easily between goal states (Ravizza & Carter, 2008); *planning* the necessary steps to achieve a goal (Smith & Jonides, 1999); and *working memory*, the ability to hold information in mind and manipulate it to guide response selection (Goldman-Rakic, 1996).

These theoretically distinct domains are supported by discrete neural systems (Luria, 1970; Shallice, 1988), which typically include elements of the prefrontal cortex (PFC). Early animal lesion studies provided evidence for PFC involvement in the coordination of complex behaviors, by serving as a temporary store for incoming information, making this information immediately available to guide response selection (Fuster, 1990; Goldman-Rakic, 1987; Jacobsen, 1936). Prefrontal damage in humans also impairs various executive functions, including planning (Owen, Downes, Sahakian, Polkey, & Robbins, 1990; Shallice, 1982, 1988), flexibility (Milner, 1982), response inhibition (Leimkuhler & Mesulam, 1985), and working memory (Milner, 1982).

Early neuroimaging and human lesion studies revealed that the frontal cortex is just one element in a network of spatially distinct regions associated with executive functions (Baddeley & Wilson, 1988). For example, neuroimaging studies of a prototypical working memory task, the *n*-back paradigm, have consistently shown activated regions in the frontal and posterior parietal cortex and cerebellum (Owen, McMillan, Laird, & Bullmore, 2005). Within this task, Broca's area and premotor cortex have been associated with subvocal rehearsal processes, while posterior parietal areas were associated with the storage of verbal information (Awh et al., 1996). On tasks that require flexibility, the ability to flexibly switch attention and behavioral responses between different rules is associated with activation of dorsolateral PFC (DLPFC), while switching attention responses between different perceptual features of a stimulus is associated with parietal activation (Ravizza & Carter, 2008).

While traditional theories of executive functions have posited a set of distinct domains supported by at least partially unique brain regions, increasing numbers of functional neuroimaging studies examining diverse executive functions have suggested that these tasks may engage very similar brain networks (e.g., Duncan & Owen, 2000). Recent views of the PFC highlight its role in higher cognitive functions by supporting coordinated activation of multiple brain areas within the "cognitive control network," including the DLPFC, medial frontal cortex (including the anterior cingulate cortex [ACC]), parietal cortex, motor areas, and cerebellum (Bellebaum & Daum, 2007; Braver, Cohen, & Barch, 2002; D'Esposito, 2007; Fuster, 2002). Furthermore, analyses of functional connectivity in healthy adults revealed that coordinated temporal activation across the network of prefrontal and posterior brain regions is associated with better performance on cognitive control tasks (Fornito, Yoon, Zalesky, Bullmore, & Carter, 2011; Yoon et al., 2008). Miller and Cohen proposed that the PFC supports "cognitive control" by actively maintaining "rules" online in order to evaluate incoming information, as well as internal states to guide response selection toward a current goal (Miller, 2000; Miller & Cohen, 2001). According to this view, cognitive control mechanisms support the range of executive functions, including working memory, selective attention, stimulus–response mapping, and performance monitoring (Carter et al., 1998; Cohen, Dunbar, & McClelland, 1990; Miyake & Shah, 1999; Shallice, 1988), and are not restricted to a particular cognitive domain (Banich, 1997; Smith & Jonides, 1999).

The diverse array of executive functions has limited our ability to directly test the unitary or modular nature of the underlying brain systems within a single set of experiments. Capitalizing on the unique power of activation likelihood estimation (ALE) meta-analytic tools, this study is the first to synthesize almost 200 published reports, testing the hypothesis that traditional executive functions are supported by a common PFC-related cognitive control network. The ALE meta-analytic approach models three-dimensional coordinates (from reported activations in standard space) as the center of a three-dimensional Gaussian distribution (Laird, Fox, et al., 2005). By combining published data from a wide variety of studies, the ALE method provides the unique opportunity to examine this question in the largest sample of control subjects published to date. Activation likelihood estimation has been has been used to address similar research questions in both healthy and patient samples (Binder, Desai, Graves, & Conant, 2009; Caspers, Zilles, Laird, & Eickhoff, 2010; Chouinard & Goodale, 2010; Dickstein, Bannon, Castellanos, & Milham, 2006; Fusar-Poli et al., 2009; Glahn et al., 2005; Goghari, 2010; Mana, Paillere Martinot, & Martinot, 2010; Minzenberg, Laird, Thelen, Carter, & Glahn, 2009; Molenberghs, Cunnington, & Mattingley, 2009; Owen et al., 2005; Ragland et al., 2009; Richlan, Kronbichler, & Wimmer, 2009; Samson, Mottron, Soulieres, & Zeffiro, 2011; Schwindt & Black, 2009; Spaniol et al., 2009; Turkeltaub & Coslett, 2010; Yu et al., 2010). We hypothesized that healthy adults would show a common pattern of activation across prefrontal (DLPFC, ACC) and parietal regions when performing executive function tasks across multiple domains (see Table 1). Furthermore, we hypothesized that additional areas of domain-specific activation may be observed, but these would occur in addition to the common pattern of activation within the cognitive control network.

Method

Study selection

A search of the BrainMap database (Fox & Lancaster, 2002; Laird, Fox, et al., 2005) was performed to identify all English-language, peer-reviewed studies that investigated executive function tasks in multiple healthy individuals,

Table 1 Definitions of the cognitive domains examined within this study, tasks included within each of the domains, the total numbers of available studies examined, and the total numbers of studies and subjects included in the present analysis, by domain and task

Cognitive Domain	Definition	Task Included in Domain	Number of Available Studies	Number of Studies Included in Current Analysis	Total Number of Subjects Included
Flexibility[1,2]	Switch from one task OR rule to another	Task switching	26	12	201
		Wisconsin Card Sorting Test	16	9	129
Inhibition[1,3]	Inhibit prepotent response in order to make correct, but less common, response	Antisaccades	13	11	149
		Flanker task	10	9	108
		Go/no-go task	40	23	417
		Simon task	12	10	192
		Stroop task	55	26	346
Working memory[4]	Maintain information/context/ temporal or spatial relationships online and manipulate or use that information to guide response selection	Complex calculation/ PASAT	39	11	152
		Delayed match to sample	24	12	150
		N-back/AXCPT	73	37	502
		Spatial span/sequence recall	20	3	24
		Sternberg task	21	15	232
Initiation[5]	Initiate sequence of complex behaviors	Word generation	85	9	115
Planning[1]	Identify and organize steps and elements needed to carry out an intention or achieve a goal	Tower Maze test	13	4	51
Vigilance[1,6]	Maintaining set in the face of interference	Oddball discrimination	10	2	64
		TOTAL =	457	193	2,832

[1] Smith and Jonides (1999). [2] Ravizza and Carter (2008). [3] Luna et al. (2010). [4] Goldman-Rakic (1996). [5] Lezak (1995). [6] Pennington and Ozonoff (1996).

ages 18–60 years, using functional magnetic resonance imaging (fMRI) or positron emission tomography (PET). Executive functions were defined as processes that are required in order to regulate or guide other cognitive processes in order to support goal-directed behavior (Minzenberg et al., 2009). For the purpose of this investigation, we examined studies that used task paradigms that are typically considered measures of executive function or cognitive control. As outlined in Table 1, these included measures of vigilance, inhibition, flexibility, planning, working memory, and initiation. Within each study, we included data from healthy individuals on specific contrasts that examined within-group whole-brain activation in response to a task of interest that was compared to an active control task, rather than to rest or fixation. Studies were excluded if the subject pool overlapped with other published studies on smaller subsets of the same sample or included subjects outside of the age range (18–60 years), if the task of interest did not require an appropriate behavioral response (e.g., a buttonpress), or if contrasts with the available coordinate data did not examine a specific executive function or rather examined differences between patients and controls. Table 1 provides the numbers of studies that were available and that met the criteria for inclusion within each domain. The BrainMap database archives the peak coordinates of activations as well as their corresponding metadata, such as the number and diagnosis of the subjects, the analysis technique, the paradigm, and the cognitive domain. Coordinates originally published in MNI space were converted to Talairach space using the Lancaster (icbm2tal) transformation (Laird et al., 2010; Lancaster et al., 2007). Further filtering and meta-analysis of the experiments was carried out using BrainMap's software applications (Laird et al., 2009), as described below.

Activation likelihood estimation

We performed a series of coordinate-based meta-analyses of executive functioning using the ALE method (Laird, McMillan, et al., 2005; Turkeltaub, Eden, Jones, & Zeffiro, 2002), in which the voxel-wise correspondence of neuroimaging results is assessed across a large number of studies. The ALE algorithm aims to identify areas showing a higher convergence of findings across experiments than would be expected under a spatially random spatial association. The identified literature coordinates were modeled with a three-dimensional Gaussian probability distribution reflecting the spatial uncertainty of each focus on the basis of an estimation of the intersubject and interlaboratory variability typically observed in neuroimaging experiments. This algorithm limits the meta-analysis to an anatomically constrained space specified by a gray-matter mask and includes a method that calculates the above-chance clustering between experiments (i.e., random-effects analysis), rather than between foci (i.e., fixed-effects analysis), and it also accounts for differences in sample sizes across the included studies (Eickhoff et al., 2009). The probabilities of all foci reported in a given experiment were combined, resulting in a modeled activation map for each experiment, and the union of these probabilities was computed in order to derive voxel-wise ALE values that described the convergence of results across the whole brain. To determine which ALE values were statistically significant, ALE scores were compared with an empirical null distribution reflecting a random spatial association between experiments, thereby estimating convergence between studies rather than the clustering of foci within a particular study.

ALE was performed in Talairach space using GingerALE 2.0 (http://brainmap.org/ale/index.html) to analyze the global set of activation foci for concordance, as well as subsets of foci that corresponded to the cognitive components of interest within executive function. From the set of included studies (Table 2), the results for a global set of within-group activations across all six domains were meta-analyzed to address the primary hypothesis. To examine the foci of greatest concordance across studies, we also performed a conjunction analysis across the three domains in which the data from more than nine studies were available (flexibility, inhibition, and working memory). To examine potential domain-specific patterns of activation, we completed within-group meta-analyses for the domains in which data from more than nine studies were available. The resultant ALE maps were thresholded at a false-discovery rate (FDR)-corrected threshold of $p < .05$. Images were viewed in Mango ("multi-image analysis GUI"), developed at the Research Imaging Institute in San Antonio (http://ric.uthscsa.edu/mango/).

Results

Global analysis across all domains

Across all domains (shown in red in Fig. 1; see also Table 3a), large clusters of significant activation were observed within lateral and medial PFC bilaterally, encompassing superior, middle, and inferior frontal gyri including the DLPFC (Brodmann areas [BAs] 9, 46), as well as the ACC (BA 32) on the medial wall. In addition to prefrontal activation, the overall contrast revealed large parietal clusters, including the inferior (BA 40) and superior (BA 7) parietal lobe. This combined frontal–parietal activation is consistent with previous findings related to the cognitive control circuit (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Carter, Botvinick, & Cohen, 1999; Cohen, Botvinick, & Carter, 2000; Yarkoni et al., 2005). Additional activation in frontal regions included the premotor cortex (BA 6), frontopolar cortex (BA 10), and orbitofrontal cortex (BA 11). Activation was also observed in occipital (BA 19) and temporal (BAs 13, 22, 37) regions, which are consistent with processing of the verbal and auditory stimuli, respectively, that are presented as part of the included tasks. Finally, significant activation was found in subcortical structures, including the thalamus, caudate, and putamen, as well as areas of the cerebellum, including the posterior declive and anterior culmen. These findings are consistent with the hypothesis that executive functions are supported by a common set of cortical and subcortical regions within the cognitive control network.

Results of the conjunction analysis (shown in green in Fig. 1; see also Table 3b) across the three domains for which the data from more than nine studies were available (flexibility, inhibition, and working memory) revealed similar patterns of common activation in cognitive-control-related frontal and parietal regions, including the DLPFC (BAs 9, 46), anterior cingulate (BA 32), inferior (BAs 39, 40) and superior (BA 7) parietal lobe, and precuneus (BA 19). The results of these analyses can be examined through an interactive viewer at http://carterlab.ucdavis.edu/research/ale_analysis.php.

Domain-specific within-group analysis

Flexibility For tasks that examined flexibility, similar patterns of activation were observed in frontal and parietal regions supporting the cognitive control network (see Fig. 2 and Table 4), including the DLPFC (BAs 9, 46), cingulate (BAs 32, 24), as well as superior (BA 7) and inferior (BA 40) parietal lobe. Activation was also observed in additional prefrontal (BAs 6, 10, 11), occipital (BA 19), and temporal (BAs 13, 37) regions.

Inhibition As is shown in Fig. 2 (see Table 5), tasks that require inhibition were associated with activation in frontal and parietal cognitive-control-related regions, including DLPFC (BAs 9, 46), ACC (BA 32), and superior (BA 7) and inferior (BA 40) parietal lobe. Such tasks also elicited activation in other prefrontal (BAs 6, 10), occipital (BA 19), and temporal (BA 13) regions. Activation of subcortical regions included the caudate, thalamus, putamen, and cerebellar declive.

Working memory Working memory tasks elicited the common pattern of frontal–parietal activation associated with the cognitive control network (see Fig. 2 and Table 6), including the DLPFC (BAs 9, 46), cingulate (BAs 32, 24), and parietal lobe (BAs 7, 40). A consistent pattern of

Table 2 Published studies included in the ALE meta-analysis of executive functions, by domain

Author	Task	PET vs. MRI	Sample Size	Age (Range or Mean)	Included Contrasts	Materials Used	Perceptual Domain
FLEXIBILITY							
K. F. Berman et al., 1995	WCST	PET	40	18–39	1. WCST > Control	Pictures (Cross Shape Array)	Visual
Brass & von Cramon, 2004	Task Switching	fMRI	14	Mean = 24	1. Meaning Switch vs. Cue Switch	Shapes	Visual
Braver, Reynolds, & Donaldson, 2003	Task Switching	fMRI	13	19–26	1. Switch × Time	Words	Visual
Cools, Clark, & Robbins, 2004	Task Switching	fMRI	16	18–45	1. Object-Rule Switch vs. Nonswitch	Pictures (Abstract Patterns)	Visual
Dove, Pollmann, Schubert, Wiggins, & von Cramon, 2000	Task Switching	fMRI	16	21–29	1. Task Switch – Task Repetition	Shapes	Visual
Dreher & Grafman, 2003	Task Switching	fMRI	8	20–31	1. Task Switching vs. Baseline	Letters	Visual
Goldberg et al., 1998	WCST	PET	12	24–39	1. WCST – Control, Activations	Pictures (Five Card Stimulus)	Visual
Kimberg, Aguirre, & D'Esposito, 2000	Task Switching	fMRI	9	College age	1. Switch – Repeat	Letters	Visual
Konishi, Nakajima, Uchida, Kameyama, et al., 1998	WCST	fMRI	7	20–31	1. Three-Dimensional – (Two- + One-Dimensional)	Pictures (Five Card Stimulus), Letters	Visual
Luks, Simpson, Feiwell, & Miller, 2002	Task Switching	fMRI	11	24–45	1. Switch > Repeat	Numbers, Shapes	Visual
Monchi, Petrides, Petre, Worsley, & Dagher, 2001	WCST	fMRI	11	18–34	1. Matching After Negative Feedback – Control Matching (Increases)	Pictures (Five Card Stimulus)	Visual
Nagahama et al., 1996	WCST	PET	18	21–35	1. Modified Card Sorting Test (MCST) vs. Matching	Pictures (Five Card Stimulus)	Visual
Nagahama et al., 1997	WCST	PET	12	21–24	1. WCST > Matching, Young	Pictures (Five Card Stimulus)	Visual
Nagahama et al., 2001	WCST	fMRI	6	Mean = 27	1. Set Shifting Task	Pictures (Three Card Stimulus)	Visual
Rao et al., 1997	WCST	fMRI	11	19–45	1. Conceptual Reasoning – Control	Words	Visual
Rogers, Andrews, Grasby, Brooks, & Robbins, 2000	WCST	PET	12	Mean = 43	1. Extradimensional (ED) – Intradimensional (ID) Shift	Shapes	Visual
Rubia et al., 2006	Task Switching	fMRI	52	20–43	1. Switch Task, Adults	Shapes	Visual
Ruff, Woodward, Laurens, & Liddle, 2001	Task Switching	fMRI	12	Mean = 23	1. Switching Color Naming, Incongruent vs. Neutral 2. Switching Word Reading, Incongruent vs. Neutral	1. Letters, Words, 2. Words	Visual
Rushworth, Hadland, Paus, & Sipila, 2002	Task Switching	fMRI	18	19–31	1. Switch – Stay, RS, Increases	Shapes	Visual
Smith, Taylor, Brammer, & Rubia, 2004	Task Switching	fMRI	20	20–43	1. Switch vs. Repeat	Shapes	Visual
Sohn, Ursu, Anderson, Stenger, & Carter, 2000	Task Switching	fMRI	12	18–36	1. Foreknowledge Effects 2. Transition Effects	Numbers, Digits	Visual
INHIBITION							
Altshuler et al., 2005	Go–No Go	fMRI	13	Mean = 31	1. No Go > Go, Normals	Letters	Visual
Asahi, Okamoto, Okada, Yamawaki, & Yokota, 2004	Go–No-Go	fMRI	17	23–30	1. Response Inhibition	Letters	Visual
Banich et al., 2000	Stroop	fMRI	10	College age	1. Incongruent > Congruent, Color	Words	Visual
Banich et al., 2001	Stroop	fMRI	14	21–35	1. Incongruent, Color vs. Neutral 2. Incongruent, Object vs. Neutral	Words	Visual
Bellgrove, Hester, & Garavan, 2004	Go–No-Go	fMRI	42	18–46	1. Response Inhibition	Letters	Visual

Table 2 (continued)

Author	Task	PET vs. MRI	Sample Size	Age (Range or Mean)	Included Contrasts	Materials Used	Perceptual Domain
Bench et al., 1993	Stroop	PET	12	21–34	1.Stroop I vs. Crosses I 2. Stroop I vs. Neutral 3. Stroop II vs. Crosses II	1. Words, Shapes 2. Words 3. Words, Shapes	Visual
G. G. Brown et al., 1999	Stroop	fMRI	8	Under age 55	1. Incongruent – Nonlexical 2. Incongruent – Neutral	1. Words, Shapes 2. Words	Visual
M. R. G. Brown, Goltz, Vilis, Ford, & Everling, 2006	Antisaccade	fMRI	10	22–33	1. Antisaccade Response > Prosaccade Response	Shapes	Visual
M. R. G. Brown, Vilis, & Everling, 2007	Antisaccade	fMRI	11	20–28	1. Preparation, Antisaccade > Preparation, Prosaccade 2. Response, Antisaccade – Preparation, Antisaccade	Shapes	Visual
Bunge et al., 2002	Flanker	fMRI	10	18–44	1. Incongruent vs. Neutral	Letters	Visual
Bush et al., 1998	Stroop	fMRI	9	Mean = 24	1. Interference – Neutral	Words	Visual
Carter, Mintun, & Cohen, 1995	Stroop	PET	15	22–49	1. Incongruent – Neutral 2. Incongruent – Congruent	Words	Visual
Chikazoe, Konishi, Asari, Jimura, & Miyashita, 2007	Antisaccade	fMRI	25	20–29	1. Antisaccade – Control Saccade	Shapes	Visual
Coderre, Filippi, Newhouse, & Dumas, 2008	Stroop	fMRI	9	18–36	1. Kana Incongruent > Kana Congruent 2. Kanji Incongruent > Kanji Congruent 3. Kana Incongruent > Kana Words 4. Kanji Incongruent > Kanji Words	Words/Symbols	Visual
de Zubicaray, Andrew, Zelaya, Williams, & Dumanoir, 2000	Go–No-Go	fMRI	8	Mean = 27	1. Effect of Decreased # of No-Go Trials 2. Linear Decreases With Number of Trials Equated per Block	Shapes	Visual
de Zubicaray, Wilson, McMahon, & Muthiah, 2001	Stroop	fMRI	8	Mean = 29	1. Semantically Related Distractor vs. Control	Words, Letters	Visual
Dichter & Belger, 2007	Flanker	fMRI	17	Mean = 25	1. Incongruent Arrows > Congruent Arrows, Controls 2. Incongruent Gaze > Congruent Gaze, Controls	1. Shapes 2. Faces	Visual
Doricchi et al., 1997	Antisaccade	PET	10	20–26	1. Antisaccades vs. Fast–Regular	Shapes	Visual
Durston et al., 2003	Flanker	fMRI	9	Mean = 26	1. Compatible Increased, Incompatible Decreased	Shapes	Visual
Ettinger et al., 2008	Antisaccade	fMRI	17	20–40	1. Saccade-by-Delay Interaction	Shapes	Visual
Fan, Flombaum, McCandliss, Thomas, & Posner, 2003	Stroop & Flanker	fMRI	12	18–34	1. Stroop Incongruent – Congruent, 2. Flanker Incongruent – Congruent	1. Words 2. Shapes	Visual
Fassbender et al., 2004	Go–No-Go	fMRI	21	19–37	1. Activations for Correct Inhibitions	Numbers	Visual
K. D. Fitzgerald et al., 2005	Flanker	fMRI	7	Mean = 30	1. High > No Interference, Normals 2. High > Low Interference, Normals	Letters	Visual
Ford, Goltz, Brown, & Everling, 2005	Antisaccade	fMRI	10	Mean = 28	1. Late Preparatory Period Comparison: Anti vs. Pro	Shapes	Visual

Table 2 (continued)

Author	Task	PET vs. MRI	Sample Size	Age (Range or Mean)	Included Contrasts	Materials Used	Perceptual Domain
Forstmann, van den Wildenberg, & Ridderinkhof, 2008	Simon	fMRI	24	Mean = 24	1. Incongruent vs. Neutral	Shapes	Visual
Garavan, Ross, & Stein, 1999	Go–No-Go	fMRI	14	19–44	1. Response Inhibition	Letters	Visual
Garavan, Ross, Murphy, Roche, & Stein, 2002	Go–No-Go	fMRI	14	19–45	1. Successful No-Gos	Letters	Visual
Garavan, Ross, Kaufman, & Stein, 2003	Go–No-Go	fMRI	16	18–46	1. Event-Related STOPS	Letters	Visual
George et al., 1993	Stroop	PET	21	Mean = 38	1. Standard Stroop – Control	Words, Shapes	Visual
Hazeltine, Bunge, Scanlon, & Gabrieli, 2003	Flanker	fMRI	10	18–44	1. Incongruent – Neutral (Conjunction of Color and Letter)	Letters, Shapes (Circle)	Visual
Heckers et al., 2004	Stroop	fMRI	15	Mean = 47	1. Interference vs. Control, Normals	Numbers, Letters/Digits	Visual
Hester et al., 2004	Go–No-Go	fMRI	15	23–40	1. Cued and Uncued Successful Response Inhibition	Letters	Visual
Horn, Dolan, Elliott, Deakin, & Woodruff, 2003	Go–No-Go	fMRI	21	18–50	1. Go/No-Go > Go	Letters	Visual
Kelly et al., 2004	Go–No-Go	fMRI	15	23–40	1. Fast and Slow Successful Response Inhibitions	Letters	Visual
Kerns et al., 2005	Stroop	fMRI	13	Mean = 36	1. Conflict-Related Activity in Normal Subjects	Words	Visual
Kerns, 2006	Simon	fMRI	26	18–36	1. Incongruent, Activations	Shapes	Visual
Kimmig et al., 2001	Antisaccade	fMRI	15	20–37	1. Prosaccade and Antisaccade	Shapes	Visual
Konishi, Nakajima, Uchida, Sekihara, & Miyashita, 1998	Go–No-Go	fMRI	5	20–31	1. No-Go Dominant Foci	Shapes	Visual
Konishi et al., 1999	Go–No-Go	fMRI	6	20–31	1. No-Go Dominant Area	Shapes	Visual
Kronhaus et al., 2006	Stroop	fMRI	11	Mean = 36	1. Incongruent Stroop > Letter String, Healthy Controls	Words, Letters	Visual
Lee, Dolan, & Critchley, 2008	Simon	fMRI	14	Mean = 24	1. Activation Associated with Interference Effect of the Simon Task	Film, Words	Visual, Auditory
Leung, Skudlarski, Gatenby, Peterson, & Gore, 2000	Stroop	fMRI	19	20–45	1. Stroop Positive	Words	Visual
Liddle, Kiehl, & Smith, 2001	Go–No-Go	fMRI	16	Mean = 30	1. Correct No-Go – Go	Letters	Visual
Liu, Banich, Jacobson, & Tanabe, 2004	Simon & Stroop	fMRI	11	24–40	1. Simon Incongruent > Simon Congruent 2. Stroop Incongruent > Stroop Congruent	Shapes	Visual
MacDonald et al., 2000	Stroop	fMRI	12	18–30	1. Color, Incongruent > Color, Congruent	Words	Visual
Maclin, Gratton, & Fabiani, 2001	Simon	fMRI	8	18–47	1. Incongruent > Congruent	Shapes	Visual
Maguire et al., 2003	Go–No-Go	fMRI	6	22–30	1. Go/No-Go vs. Go	Shapes	Visual
Maltby, Tolin, Worhunsky, O'Keefe, & Kiehl, 2005	Go–No-Go	fMRI	14	Mean = 37	1. Correct Inhibition, Normals	Letters	Visual
Matsuda et al., 2004	Antisaccade	fMRI	21	Mean = 39	1. Antisaccades > Saccades	Shapes	Visual
Mead et al., 2002	Stroop	fMRI	18	18–46	1. Incongruent > Congruent 2. Incongruent > Neutral	Words	Visual
Menon, Adelman, White, Glover, & Reiss, 2001	Go–No-Go	fMRI	14	17–41	1. Go/No-Go – Go	Letters	Visual

Table 2 (continued)

Author	Task	PET vs. MRI	Sample Size	Age (Range or Mean)	Included Contrasts	Materials Used	Perceptual Domain
Milham et al., 2001	Stroop	fMRI	16	18–30	1. Incongruent > Neutral	Words	Visual
Milham et al., 2002	Stroop	fMRI	22	21–27	1. Incongruent > Congruent or Neutral, Young Subjects	Words	Visual
Milham & Banich, 2005	Stroop	fMRI	18	18–40	1. Incongruent vs. Congruent	Words	Visual
Mostofsky et al., 2003	Go–No-Go	fMRI	48	Mean = 27	1. Primary No-Go Effects 2. Primary Counting No-Go Effects	Pictures (Spaceships)	Visual
Norris, Zysset, Mildner, & Wiggins, 2002	Stroop	fMRI	7	23–31	1. Incongruent vs. Neutral, GE-EPI, Activations	Words, Letters	Visual
O'Driscoll et al., 1995	Antisaccade	PET	10	22–39	1. Antisaccade – Saccade	Shapes	Visual
Paus, Petrides, Evans, & Meyer, 1993	Antisaccade	PET	9	19–30	1. Oculomotor, Antistimulus – Prostimulus	Shapes	Visual
Peterson et al., 2002	Simon & Stroop	fMRI	10	24–29	1. Simon Incongruent vs. Congruent 2. Stroop Incongruent vs. Congruent	1. Shapes 2. Words	Visual
Roth et al., 2006	Stroop	fMRI	11	18–55	1. Incongruent > Congruent, Normals	Words	Visual
Roth et al., 2007	Go–No Go	fMRI	14	Mean = 38	1. Response Inhibition, Normals	Shapes	Visual
Rubia et al., 2001	Go–No-Go	fMRI	15	26–58	1. Generic Go/No-Go Activation 2. Generic Stop Activation	Pictures (Planes, Airplanes Bombs)	Visual
Rubia et al., 2006	Go–No-Go & Simon	fMRI	52	10–43	1. Go/No-Go Task, Adults 2. Simon Task, Adults	Shapes	Visual
Sommer, Hajak, Döhnel, Meinhardt, & Müller, 2008	Simon	fMRI	12	22–37	1. Incompatible > Compatible	Letters	Visual
Sweeney et al., 1996	Antisaccade	PET	11	Mean = 27	1. Antisaccades – Visually Guided Saccades, Increases 2. Conditional Antisaccades – Visually Guided Saccades, Increases	Shapes	Visual
Tang, Critchley, Glaser, Dolan, & Butterworth, 2006	Stroop	fMRI	18	21–38	1. Numerical Task Conflict Trials > Numerical Task Nonconflict Trials 2. Physical Task Conflict Trials > Physical Task Nonconflict Trials	Numbers	Visual
Taylor, Kornblum, Lauber, Minoshima, & Koeppe, 1997	Stroop	PET	18	Under age 30	1. Stroop – Neutral Words	Words	Visual
Ullsperger & von Cramon, 2001	Flanker	fMRI	12	21–29	1. Response Competition (Incompatible Correct vs. Compatible Correct)	Shapes	Visual
van Veen, Cohen, Botvinick, Stenger, & Carter, 2001	Flanker	fMRI	12	Mean = 27	1. (Congruent = Stimulus Incongruent) < Response Incongruent 2. Congruent < Stimulus Incongruent < Response Incongruent	Letters	Visual
Vink et al., 2005	Go–No-Go	fMRI	20	Mean = 20	1. Go/Stop > Go Only 2. Parametric Analysis	Shapes	Visual
Watanabe et al., 2002	Go–No-Go	fMRI	11	19–40	1. Specific Activation Areas During NO-GO Phase	Shapes	Visual
Wittfoth, Buck, Fahle, & Herrmann, 2006	Simon	fMRI	20	21–31	1. Motion-Based: Incompatible > Compatible 2. Location-Based: Incompatible > Compatible	Shapes	Visual

Table 2 (continued)

Author	Task	PET vs. MRI	Sample Size	Age (Range or Mean)	Included Contrasts	Materials Used	Perceptual Domain
Wittfoth, Kustermann, Fahle, & Herrmann, 2008	Simon	fMRI	15	21–31	1. Incompatible > Compatible	Shapes	Visual
Yücel et al., 2007	Flanker	fMRI	19	Mean = 31	1. Incongruent > Congruent, Normals	Numbers	Visual
Zysset, Muller, Lohmann, & von Cramon, 2001	Stroop	fMRI	9	21–34	1. Incongruent vs. Neutral 2. Incongruent vs. Congruent	1. Words, Letters 2. Words	Visual
WORKING MEMORY							
Audoin et al., 2005	Complex Calculation	fMRI	18	19–40	1. PASAT – REPEAT, Controls	Numbers	Auditory
Awh et al., 1996	Sternberg & *N*-back	PET	20	18–27	1. Sternberg Item Recognition Memory – Control 2. 2-Back – Search Control	Letters	Visual
Barch et al., 2001	*N*-back	fMRI	12	Mean = 25	1. Main Effect of Delay	Letters	Visual
Bedwell et al., 2005	Sternberg	fMRI	14	22–40	1. Brain regions significantly active during encoding period 2. Brain regions significantly active during retrieval period	Letters	Visual
Braver et al., 1997	*N*-back	fMRI	8	18–25	1. Brain Areas Showing Monotonic Increases in Activity as a Function of Memory Load	Letters	Visual
Bunge, Ochsner, Desmond, Glover, & Gabrieli, 2001	Sternberg	fMRI	16	18–40	1. Load 6 > Load 4	Letters	Visual
Cairo, Liddle, Woodward, & Ngan, 2004	Sternberg	fMRI	18	18–35	1. Encoding, Linear Regression with Load 2. Retrieval, Linear Regression with Load	Letters	Visual
Callicott et al., 1999	*N*-back	fMRI	9	18–39	1. Significant Increases in Activation as a Function of Working Memory Load	Numbers	Visual
Carlson et al., 1998	*N*-back	fMRI	7	17–23	1. Two-Back vs. Zero-Back 2. One-Back vs. Zero-Back 3. Two-Back vs. One-Back	Shapes	Visual
Casey et al., 1998	*N*-back	fMRI	32	19–43	1. Memory – Motor, Pooled Data	Shapes	Visual
Chen et al., 2004	Delayed Match to Sample	fMRI	8	Mean = 28	1. Verbal Working Memory 2. Visual Abstract Working Memory	1. Words 2. Pictures (Abstract Patterns)	1. Visual 2. Shapes
Clark et al., 2000	*N*-back	PET	10	Mean = 47	1. Variable Target > Fixed Target	Words	Visual
Cohen et al., 1994	*N*-back	fMRI	12	20–29	1. Memory – Control	Letters	Visual
Cohen et al., 1997	*N*-back	fMRI	10	18–34	1. Load 2. Load × Time	Letters	Visual
Crespo-Facorro et al., 2001	Delayed Match to Sample	PET	34	Mean = 26	1. Novel – Well-learned, Normals	Shapes	Visual
Dade, Zatorre, Evans, & Jones-Gotman, 2001	*N*-back	PET	12	20–30	1. Odor Working Memory – Baseline 2. Face Working Memory – Baseline	1. Scent 2. Faces	1. Ofactory, 2. Visual
Delazer et al., 2003	Complex Calculation	fMRI	13	Mean = 31	1. Untrained vs. Trained Multiplication Set	Numbers	Visual
Dolcos & McCarthy, 2006	Delayed Match to Sample	fMRI	15	18–31	1. Neutral – Scrambled Pictures	Faces	Visual

Table 2 (continued)

Author	Task	PET vs. MRI	Sample Size	Age (Range or Mean)	Included Contrasts	Materials Used	Perceptual Domain
Druzgal & D'Esposito, 2001a	*N*-back	fMRI	9	21–27	1. Match > No Match	Faces	Visual
Druzgal & D'Esposito, 2001b	Sternberg	fMRI	9	22–27	1. Working Memory Load	Faces	Visual
Fehr, Code, & Hermann, 2007	Complex Calculation	fMRI	11	22–40	1. Addition, Complex > Simple 2. Subtraction, Complex > Simple 3. Multiplication, Complex > Simple 4. Division, Complex > Simple 5. Conjunction (All Conditions)	Numbers	Visual
Garavan, Kelley, Rosen, Rao, & Stein, 2000	Delayed Match to Sample	fMRI	17	Mean = 26.6	1. Visual working memory vs. Control	Shapes	Visual
Garavan, Ross, Li, & Stein, 2000	Complex Calculation	fMRI	11	19–41	1. Function of Switching Frequency	Shapes	Visual
Ghatan, Hsieh, Petersson, Stone-Elander, & Ingvar, 1998	Complex Calculation	PET	6	20–24	1. Irrelevant Speech + Arithmetical Task vs. Arithmetical Task (Increase in rCBF)	Words & Digits	Auditory & Visual
Harvey et al., 2005	*N*-back	fMRI	10	18–45	1. *n*-Back vs. 0-Back, Healthy Subjects	Letters	Visual
Honey et al., 2003	*N*-back	fMRI	27	Mean = 35	1. Working Memory, Normals	Letters	Visual
Hugdahl et al., 2004	Complex Calculation	fMRI	12	Mean = 31	1. Mental Arithmetic – Vigilance, Healthy Subjects	Numbers	Visual
Ischebeck et al., 2006	Complex Calculation	fMRI	12	Mean = 27	1. Multiplication Untrained vs. Number Matching 2. Subtraction Untrained vs. Number Matching	Numbers	Visual
Johnson et al., 2006	Sternberg	fMRI	18	Mean = 37	1. Controls, Activation Modulated by Load, Encoding 2. Controls, Activation Modulated by Load, Retrieval 3. Controls, Difficult 6 > Medium 6, Encoding 4. Controls, Difficult 6 > Medium 6, Retrieval	Letters	Visual
Jonides et al., 1997	*N*-back	PET	19	College age	1. 3-back minus Control, Activations 2. 2-back minus Control, Activations 3. 1-back minus Control, Activations 4. 0-back minus Control, Activations	Letters	Visual
Kim et al., 2002	*N*-back	PET	14	Mean = 25	1. Simple Pictures – Control 2. Korean Words – Control	1. Shapes 2. Words	Visual
Kim et al., 2003	*N*-back	fMRI	12	19–35	1. 2-Back – Control, Normals	Shapes	Visual
Kirschen, Chen, Schraedley-Desmond, & Desmond, 2005	Sternberg	fMRI	16	Mean = 25	1. Linear Activations (effect of increasing load)	Letters	Visual
Kumari et al., 2006	*N*-back	fMRI	13	18–55	1. 1 Back > 0 Back, Normals 2. 2 Back > 0 Back, Normals	Shapes	Visual
LaBar, Gitelman, Parrish, & Mesulam, 1999	*N*-back	fMRI	11	Mean = 33	1. Working Memory	Letters	Visual
Lagopoulos, Ivanovski, & Malhi, 2007	Sternberg	fMRI	10	20–54	1. Encoding, Healthy Controls	Words	Visual

Table 2 (continued)

Author	Task	PET vs. MRI	Sample Size	Age (Range or Mean)	Included Contrasts	Materials Used	Perceptual Domain
					2. Response, Healthy Controls		
Landau, Schumacher, Garavan, Druzgal, & D'Esposito, 2004	Delayed Match to Sample	fMRI	10	22–27	1. Encoding: Main Effect Only 2. Retrieval: Main Effect Only	Faces	Visual
Lange et al., 2005	Complex Calculation	fMRI	44	21–45	1. mPASAT vs. Auditory Monitoring using a random effects model, Controls	Numbers	Auditory
Lazeron, Rombouts, de Sonneville, Barkhof, & Scheltens, 2003	Complex Calculation	fMRI	9	19–30	1. High (rapid math) vs. Low (slow simple math)	Numbers	Visual
Leung, Gore, & Goldman-Rakic, 2002	Delayed Match to Sample	fMRI	6	Mean = 28	1. Late Delay 2. Main Task Effects	Shapes	Visual
					3. Time Effects		
					4. Interaction Between Task and Time		
Linden et al., 2003	Sternberg	fMRI	12	24–31	1. Encoding	Shapes	Visual
MacDonald & Carter, 2003	*N*-back	fMRI	17	Mean = 34	1. Cue by Scan Interaction, Normals	Letters	Visual
MacDonald et al., 2005	*N*-back	fMRI	28	Mean = 25	1. Nontarget vs. Target, Normals 2. Long vs. Short Delay, Normals	Letters	Visual
Manoach et al., 2000	Delayed Match to Sample	fMRI	9	28–49	1. 5 Targets WM vs. Arrows, Normals	Numbers, Shapes	Visual
Martinkauppi, Rama, Aronen, Korvenoja, & Carlson, 2000	*N*-back	fMRI	10	20–30	1. 3-Back vs. 1-Back 2. 2-Back vs. 1-Back	Tones	Auditory
Matsuo et al., 2007	*N*-back	fMRI	15	Mean = 38	1. 1-back > 0-back, Normals 2. 2-back > 0-back, Normals	Numbers	Visual
Mayer et al., 2007	Delayed Match to Sample	fMRI	18	20–44	1. Working Memory Selective, WM Load	Shapes	Visual
Mendrek et al., 2005	*N*-back	fMRI	12	Mean = 28	1. Activations, 2-Back vs. 0-Back, Normals	Letters	Visual
Menon, Anagnoson, Mathalon, Glover, & Pfefferbaum, 2001	*N*-back	fMRI	13	37–49	1. Average Group Activation For Controls	Numbers	Auditory
Monks et al., 2004	*N*-back & Sternberg	fMRI	12	Mean = 46	1. 2-Back vs. Baseline, Controls 2. Sternberg, Controls	1. Letters 2. Numbers	Visual
Owen et al., 1998	*N*-back	fMRI	6	College age	1. Spatial Working Memory vs. Control 2. Nonspatial Working Memory vs. Control	1. Shapes 2. Pictures (Abstract Patterns)	Visual
Owen et al., 1999	*N*-back & Sequencing	PET	5	44–55	1. Spatial Manipulation – Visuomotor Control 2. Spatial Span – Visuomotor Control	Shapes	Visual
Perlstein, Dixit, Carter, Noll, & Cohen, 2003	*N*-back	fMRI	15	26–47	1. *N*-Back Load Main Effect 2. AX-CPT Cue Type Main Effect	Letters	Visual
Petit, Courtney, Ungerleider, & Haxby, 1998	Delayed Match to Sample	fMRI	12	Mean = 28	1. Spatial Working Memory 2. Face Working Memory	Faces	Visual
Petrides, Alivisatos, Meyer, & Evans, 1993	Complex Calculation	PET	10	19–39	1. Self-Ordered – Counting 2. Externally Ordered – Counting	Numbers	Auditory
Pochon et al., 2001	*N*-back & Sequencing	fMRI	8	20–25	1. Visuospatial matching (MAT) vs. Control (MAT CONT)	Shapes	Visual

Table 2 (continued)

Author	Task	PET vs. MRI	Sample Size	Age (Range or Mean)	Included Contrasts	Materials Used	Perceptual Domain
					2. Visuospatial reproduction (REP) vs. Control (REP CONT)		
Ragland et al., 2002	*N*-back	fMRI	11	21–53	1. Letter 1-Back – 0-Back 2. Fractal 1-Back – 0-Back 3. Letter 2-Back – 0-Back 4. Fractal 2-Back – 0-Back 5. Letter 2-Back – 1-Back 6. Fractal 2-Back – 1-Back	1. Letters 2. Shapes (Fractals) 3. Letters 4. Shapes 5. Letters 6. Shapes (Fractals)	Visual
Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000	Delayed Match to Sample	fMRI	6	24–34	1. Working Memory Maintenance 2. Selection from Memory	Shapes	Visual
Rypma, Prabhakaran, Desmond, Glover, & Gabrieli, 1999	Sternberg	fMRI	6	Mean = 25	1. 3–1 Contrast 2. 6–1 Contrast	Letters	Visual
Rypma, Prabhakaran, Desmond, & Gabrieli, 2001	Sternberg	fMRI	12	22–29	1. Sternberg, Load 6 vs. Load 1, Young Subjects	Letters	Visual
Sánchez-Cárrion et al., 2008	*N*-back	fMRI	14	Mean = 24	1. 2-back vs. 0-back, Normals 2. 3-back vs. 0-back, Normals	Numbers	Visual
Schumacher et al., 1996	*N*-back	PET	8	Under age 60	1. Visual Memory – Control, Increases 2. Auditory Memory – Control, Increases	1. Letters 2. Letters	1. Visual 2. Auditory
Sheridan, Hinshaw, & D'Esposito, 2007	Delayed Match to Sample	fMRI	10	12–17	1. Encoding, High Load > Low Load, Normals	Letters	Visual
Smith, Jonides, & Koeppe, 1996	*N*-back & Sternberg	PET	30	College age	1. Verbal 3-Back – Control 2. Spatial 3-Back – Control 3. Verbal 2-Back – Control 4. Verbal Memory – Control 5. Spatial Memory – Control	1. Letters 2. Letters 3. Letters 4. Letters, Shapes 5. Letters, Shapes	Visual
Stern et al., 2000	Delayed Match to Sample	fMRI	5	Missing	1. Working Memory I vs. Control 2. Working Memory II vs. Control 3. Working Memory I vs. Working Memory II	Pictures (Abstract Patterns)	Visual
van der Wee et al., 2003	*N*-back	fMRI	11	Mean = 35	1. 1 + 2 + 3-Back vs. 0-Back, Normals	Shapes	Visual
Veltman, Rombouts, & Dolan, 2003	*N*-back & Sternberg	fMRI	22	Mean = 23	1. *n*-Back vs. Control 2. Sternberg vs. Control	Letters	Visual
Volle et al., 2005	Sequencing	fMRI	11	22–34	1. MemG Delay One, 3 Square vs. 1 Square 2. MemG Delay One, 5 Square vs. 3 Square 3. MemG Delay Two vs. VisG Delay Two	Shapes	Visual
Walter, Wolf, Spitzer, & Vasic, 2007	Sternberg	fMRI	17	Mean = 31	1. Load 1 > Simple Reaction, Normals 2. Load 2 > Simple Reaction, Normals 3. Load 3 > Simple Reaction, Normals	Letters	Visual
Yoo et al., 2005	*N*-back	fMRI	10	20–30	1. Working Memory, Normals	Faces, Abstract Patterns	Visual

Table 2 (continued)

Author	Task	PET vs. MRI	Sample Size	Age (Range or Mean)	Included Contrasts	Materials Used	Perceptual Domain
Zago et al., 2001	Complex Calculation	PET	6	Mean = 21	1. Compute (complex math) vs. Read	Numbers	Visual
Zurowski et al., 2002	*N*-back	PET	8	Mean = 27	1. Main Effect of Working Memory	Syllables	Visual
INITIATION							
Audenaert et al., 2000	Word Generation	fMRI	20	19–28	1. Letter Fluency vs. Control 2. Category Fluency vs. Control	1. Letters, Words 2. Words	Auditory
Basho, Palmer, Rubio, Wulfeck, & Muller, 2007	Word Generation	fMRI	12	21–37	1. Factor-Specific Effects for Overt	Words	Auditory, Visual
Crosson et al., 1999	Word Generation	fMRI	17	28–32	1. Emotionally Neutral words – Repetition	Words	Auditory
Frith, Friston, Liddle, & Frackowiak, 1991	Word Generation	PET	6	25–45	1. Fixed Words, Generate – Random Words, Repeat	Words	Auditory
Fu et al., 2002	Word Generation	fMRI	11	Mean = 30	1. Easy Letter Fluency vs. Repetition 2. Difficult Letter Fluency vs. Repetition	Letters	Visual
Klein, Milner, Zatorre, Meyer, & Evans, 1995	Word Generation	PET	12	Mean = 22	1. L1 Synonym Generation – L1 Word Repeating	Words	Auditory
Klein, Milner, Zatorre, Zhao, & Nikelski, 1999	Word Generation	PET	13	18–28	1. Verb Generation minus Word Repetition (Chinese words)	Words	Auditory
Petersen, Fox, Posner, Mintun, & Raichle, 1988	Word Generation	PET	17	Under age 40	1. Generate Words – Repeat Words, Visual 2. Generate Words – Repeat Words, Auditory	Words	
Petersen, Fox, Posner, Mintun, & Raichle, 1989	Word Generation	PET	7	18–49	1. Generate Verbs, Visual vs. Repeat Words, Visual 2. Generate Verbs, Auditory vs. Repeat Words, Auditory	Words	1. Visual 2. Auditory
PLANNING							
Fincham, Carter, van Veen, Stenger, & Anderson, 2002	Tower Test	fMRI	8	18–32	1. Planning (Tower vs. control)	Numbers	Visual
P. B. Fitzgerald et al., 2008	Tower Test	fMRI	13	Mean = 35	1. Regions Correlated with Reaction Time During TOL Task in Controls	Shapes	Visual
Ghatan et al., 1995	Maze Task	PET	8	41–59	1. Perceptual Maze vs. Motor Control, Increase in rCBF	Shapes	Visual
van den Heuvel et al., 2005	Tower Test	fMRI	22	Mean = 30	1. Planning (Tower) vs. Counting, Normals 2. Increases Correlating With Increased Task Load, Normals	Shapes	Visual
VIGILANCE							
Gur et al., 2007	Oddball	fMRI	36	18–48	1. Target Green Circles > Standard Red Circles	Shapes	Visual
Laurens, Kiehl, Ngan, & Liddle, 2005	Oddball	fMRI	28	Mean = 28	1. Novel Stimuli vs. Nontarget Stimuli, Controls	Tones	Auditory

WCST, Wisconsin Card Sort task.

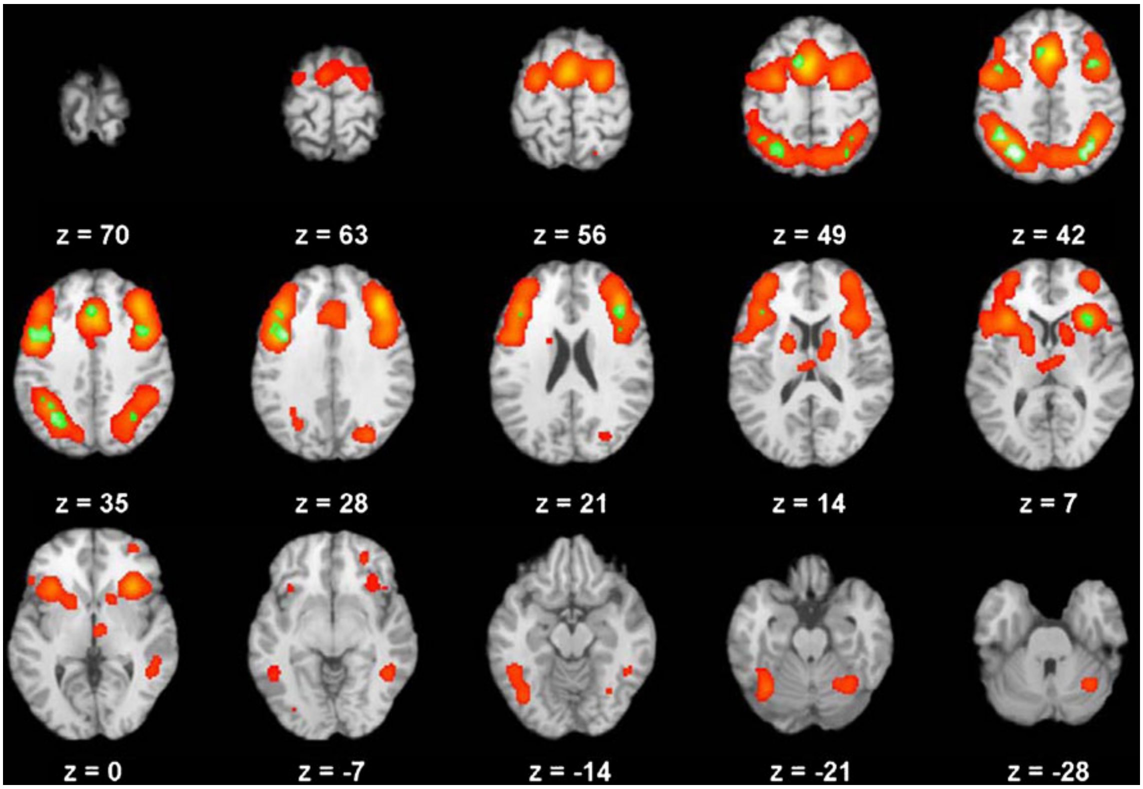

Fig. 1 Global analysis of executive function in 193 studies of healthy adults, showing brain regions with significant activation across all executive function domains (red) and the areas of conjunction (green) across the three domains for which data from more than nine studies were available (flexibility, inhibition, and working memory).

activation was also observed in prefrontal (BAs 6, 10), occipital (BA 19), temporal (BAs 13, 37), and subcortical (thalamus, caudate, putamen, cerebellar declive) regions.

Other domains Domain-specific analyses for the planning and vigilance domains were not possible, due to the small number of studies available for inclusion within the ALE analysis (four and two studies, respectively). Although the number of studies for the initiation domain was also small (n = 9), the results are presented here as a preliminary analysis of site-specific activation within this domain. In contrast to the pattern of frontal–parietal activation observed in the other three domains, initiation tasks were associated with a pattern of activation primarily in frontal regions, including the DLPFC (BA 46), middle (BA 10) and inferior (BA 47) frontal, anterior cingulate (BA 32), and motor (BA 6) regions, with no observed activation in parietal regions (see Fig. 2, Table 7). Activation was also observed in the superior (BA 21) and middle (BA 22) temporal, occipital (BA 17), and subcortical (putamen, caudate, cerebellar declive and culmen) regions, in a manner similar to other executive domains.

Discussion

Using a meta-analytic approach, we examined 193 neuroimaging studies of tasks divided according to classic executive function domains, creating the largest sample of healthy adults to date. We sought to provide evidence that discrete executive functions (initiation, inhibition, working memory, flexibility, planning, and vigilance) are supported by a shared, superordinate network that has been previously associated with cognitive control. Results of the combined analysis across domains showed that executive functions are indeed associated with increased activity in this common cognitive control network (Bellebaum & Daum, 2007; Botvinick et al., 2001; Carter et al., 1999; Cohen et al., 2000; D'Esposito & Postle, 2002; Yarkoni et al., 2005), which includes the DLPFC (BAs 9, 46), frontopolar cortex (BA 10), orbitofrontal cortex (BA 11), and anterior cingulate (BA 32). Additional concurrent regions of activation included the superior and inferior parietal (BAs 7, 40), occipital (BA 19), and temporal (BAs 13, 22, 37) cortex, as well as subcortical areas including the caudate, putamen, thalamus, and cerebellum. These conclusions were further supported by a conjunction analysis across the three domains in which data from more than nine studies were

Table 3 Brain regions (Brodmann areas in parentheses) with significant activation within healthy adults from (a) a combined meta-analysis across all six executive function domains and (b) a conjunction meta-analysis for domains with more than nine included studies (flexibility, inhibition, and working memory)

		Maxima		
Brain Region (BA)	Volume (mm^3)	*x*	*y*	*z*
(a) Combined Across All Six Domains				
Right Middle Frontal Gyrus (9)	20,048	40	30	28
Right Insula (13)		32	18	4
Right Middle Frontal Gyrus (10)		32	48	14
Right Inferior Parietal Lobule (40)	12,328	38	–50	42
Right Superior Parietal Lobule (7)		32	–60	42
Right Cuneus (19)		28	–76	28
Left Superior Parietal Lobule (7)	11,200	–28	–60	44
Right Precuneus (7)		8	–68	46
Left Precuneus (7)		–6	–62	44
Left Superior Frontal Gyrus (6)	9,112	–2	6	50
Left Insula (13)	6,744	–32	18	6
Left Cerebellar Declive	4,592	–34	–62	–20
Left Fusiform Gyrus (37)		–46	–50	–12
Left Middle Frontal Gyrus (10)	3,608	–36	44	18
Right Frontal Lobe Subgyral (6)	3,032	26	–2	54
Right Caudate Body	2,984	16	2	12
Right Thalamus		12	–8	14
Right Thalamus		6	–16	2
Left Inferior Frontal Gyrus (9)	2,776	–42	4	30
Left Middle Frontal Gyrus (9)	2,480	–40	26	28
Right Cerebellar Culmen	2,352	32	–60	–24
Left Middle Frontal Gyrus (6)	1,936	–28	–4	50
Right Temporal Lobe Subgyral (37)	1,912	46	–52	–6
Right Middle Temporal Gyrus (22)		50	–42	2
Right Inferior Frontal Gyrus (9)	1,080	44	6	32
Left Lentiform Nucleus Putamen	1,016	–20	8	4
Left Inferior Parietal Lobule (40)	864	–38	–52	40
Right Caudate Head	808	14	10	4
Right Cingulate Gyrus (32)	704	2	16	40
Left Thalamus	296	–2	–20	10
Right Middle Frontal Gyrus (11)	224	26	42	–10
Left Fusiform Gyrus (19)	128	–28	–80	–12
Left Lentiform Nucleus Putamen	128	–18	–2	12
(b) Conjunction Analysis				
(Flexibility, Inhibition, and Working Memory)				
Left Superior Parietal Lobule (7)	1,896	–26	–64	40
Left Inferior Frontal Gyrus (9)	1,880	–38	6	28
Left Middle Frontal Gyrus (9)		–48	6	36
Left Middle Frontal Gyrus (9)		–46	14	28
Left Middle Frontal Gyrus (9)		–42	22	28
Right Inferior Parietal Lobule (39)	856	34	–62	40
Right Precuneus (19)		30	–66	44
Right Middle Frontal Gyrus (6)	576	34	8	42
Right Precentral Gyrus (9)		40	8	36
Left Inferior Parietal Lobule (40)	568	–38	–52	44
Left Superior Frontal Gyrus (6)	528	–8	10	48
Left Cingulate Gyrus (32)		–6	18	42
Right Middle Frontal Gyrus (46)	432	40	26	22

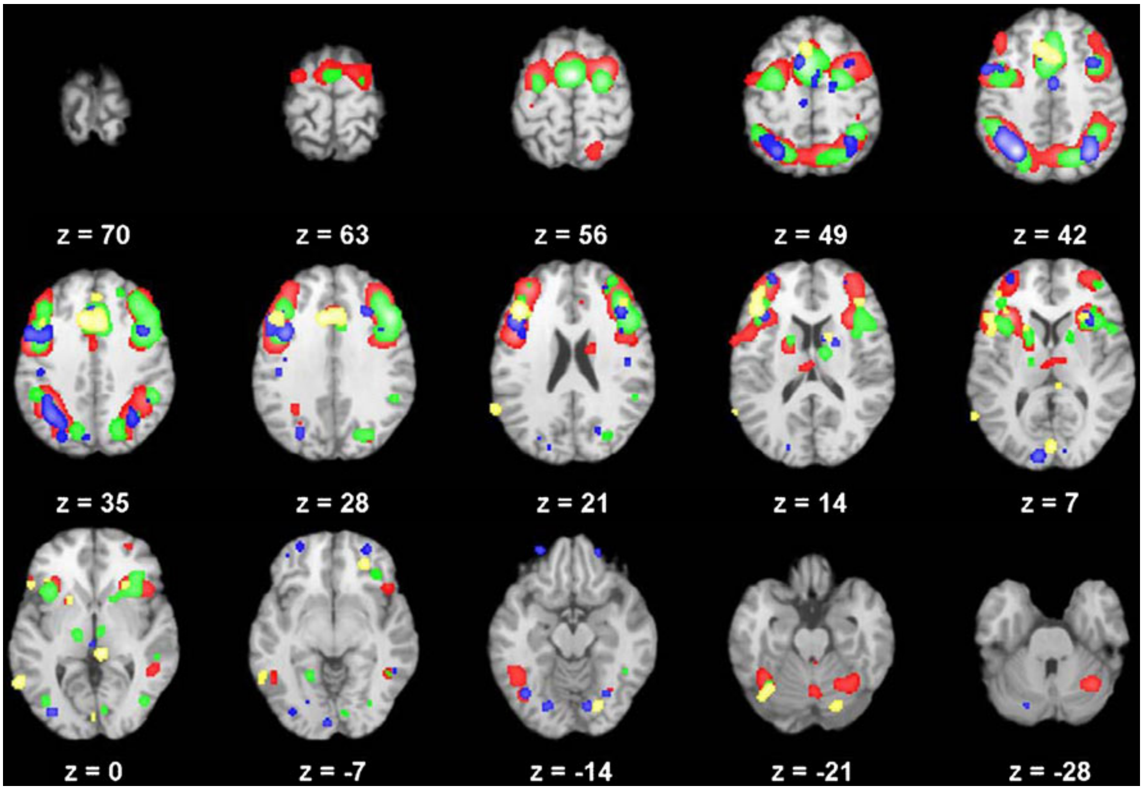

Fig. 2 Domain-specific analysis showing patterns of common and distinct activation across the working memory (red; 78 studies), inhibition (green; 79 studies), flexibility (blue; 21 studies), and initiation (yellow; 9 studies) domains

available (flexibility, inhibition, and working memory), which revealed a similar pattern of common activation in cognitive-control-related frontal and parietal regions. Although the present analysis did not directly examine the functional connectivity of these brain regions during each task, previous studies of cognitive control (Fornito et al., 2011; Yoon et al., 2008) have consistently shown task-related increases in functional connectivity between the DLPFC and the network of brain regions shown here.

These results provide additional evidence that a superordinate cognitive control network supports executive functions across a range of "domains" previously considered to be distinct, including flexibility, working memory, initiation, and inhibition. As proposed by Miller and Cohen (2001), it has been common to stress the distributed nature of the network that supports cognitive control functions, as well as the unique functional contributions by specific regions within the network. Within this framework, elements of the network may be differentially engaged, depending on the task demands. For example, previous studies (Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010; Vincent, Kahn, Snyder, Raichle, & Buckner, 2008) have shown that the frontoparietal control network is engaged across multiple goal-directed activities, flexibly engaging the default-mode network to support autobiographical planning, or engaging the dorsal attention network to support visual spatial planning. Similarly, demands for specific goal- or task-context-related activity may be associated with stronger engagement of the PFC, and demands for maintaining information over longer periods of time may lead to more sustained network activity (Dosenbach et al., 2006; Yarkoni, Barch, Gray, Conturo, & Braver, 2009). Its connectivity with sensory and motor regions, including the cerebellum, allows the DLPFC to play a central role in the maintenance of the rules for action, as well as response selection and inhibition (Asaad, Rainer, & Miller, 2000; Bellebaum & Daum, 2007; Watanabe, 1990, 1992). The ACC and related medial frontal regions are considered to support cognitive control by detecting conditions, such as processing conflicts, that indicate the demand for control, which then leads to the engagement of the DLPFC (Egner & Hirsch, 2005; Kerns et al., 2005; MacDonald, Cohen, Stenger, & Carter, 2000). Furthermore, parietal activation is considered to provide the DLPFC with information on stimulus salience and learned stimulus–response pairings, while the DLPFC is thought to support its ability to shift attentional focus according to the demands of the task at hand (Bunge, Hazeltine, Scanlon, Rosen, & Gabrieli, 2002; Bunge, Kahn, Wallis, Miller, & Wagner, 2003; Miller & Cohen, 2001; Posner & Petersen, 1990).

Table 4 Brain regions (Brodmann areas in parentheses) with significant activation within healthy adults for tasks within the flexibility domain

		Maxima		
Brain Region (BA)	Volume (mm^3)	*x*	*y*	*z*
Left Inferior Frontal Gyrus (9)	6,472	–38	6	28
Left Middle Frontal Gyrus (46)		–46	18	24
Left Middle Frontal Gyrus (9)		–50	6	36
Left Middle Frontal Gyrus (46)		–42	26	16
Left Superior Parietal Lobule (7)	6,328	–26	–62	44
Left Inferior Parietal Lobule (40)		–36	–54	42
Left Precuneus (19)		–26	–78	32
Right Precuneus (19)	2,648	32	–64	42
Right Middle Frontal Gyrus (6)	1,176	34	8	44
Right Precentral Gyrus (9)		40	8	36
Right Inferior Frontal Gyrus (9)		40	10	24
Right Middle Frontal Gyrus (46)	856	40	26	22
Right Middle Frontal Gyrus (9)		28	24	30
Left Superior Frontal Gyrus (6)	688	–8	10	48
Left Cingulate Gyrus (32)		–6	18	42
Right Cingulate Gyrus (24)	584	4	–8	44
Right Medial Frontal Gyrus (6)		6	0	48
Left Fusiform Gyrus (19)	544	–38	–68	–14
Left Cerebellar Declive		–38	–68	–18
Left Cuneus (17)	544	–10	–92	8
Left Middle Frontal Gyrus (10)	464	–32	52	10
Right Middle Frontal Gyrus (11)	408	22	46	–12
Right Middle Frontal Gyrus (10)		28	50	–8
Left Middle Frontal Gyrus (11)	408	–26	48	–12
Left Inferior Occipital Gyrus (18)	368	–32	–82	–2
Right Insula (13)	344	32	18	8
Left Cerebellar Declive	328	–20	–78	–16
Left Cingulate Gyrus (32)	296	0	26	36
Right Lentiform Nucleus Putamen	272	20	0	14
Right Caudate Body		10	4	16
Left Postcentral Gyrus (2)	240	–42	–24	30
Right Cerebellar Declive	208	12	–78	–14
Right Medial Frontal Gyrus (6)	208	18	–10	52
Right Cuneus (18)	152	24	–76	16
Right Precuneus (31)		22	–70	24
Left Middle Occipital Gyrus (18)	144	–18	–86	16
Left Lingual Gyrus (18)	136	–4	–90	–8
Right Temporal Lobe Sub-Gyral (37)	104	50	–48	–10
Left Paracentral Lobule (6)	104	–6	–24	52

Within the cognitive control network, it is likely that network-level subdivisions also exist and may be differentially engaged in the same manner. For example, Dosenbach, Fair, Cohen, Schlaggar, and Petersen (2008) proposed discrete circuits within this broader network that support task-sustained versus transient aspects of control, and that these networks may be differentially engaged across different forms of executive functions. Similarly, Braver, Paxton, Locke, and Barch (2009) emphasized that cognitive control has proactive and reactive elements. Proactive control may also depend more on sustained activity in the cognitive control network and, to the degree that

Table 5 Brain regions (Brodmann areas in parentheses) with significant activation within healthy adults for tasks within the inhibition domain

Brain Region (BA)	Volume (mm³)	Maxima		
		x	*y*	*z*
Right Middle Frontal Gyrus (9)	20,464	46	20	28
Right Middle Frontal Gyrus (46)		40	32	24
Right Middle Frontal Gyrus (9)		38	28	32
Right Inferior Frontal Gyrus (9)		46	6	32
Right Precentral Gyrus (9)		38	6	38
Right Claustrum		32	16	2
Right Inferior Frontal Gyrus (47)		34	26	0
Right Precentral Gyrus (44)		50	10	8
Right Lentiform Nucleus Putamen		16	2	10
Right Lentiform Nucleus Putamen		16	8	2
Left Medial Frontal Gyrus (6)	15,872	0	–2	56
Left Medial Frontal Gyrus (32)		0	10	46
Left Precentral Gyrus (9)	13,368	–42	4	32
Left Middle Frontal Gyrus (6)		–28	–4	50
Left Middle Frontal Gyrus (9)		–40	28	32
Left Insula (13)		–36	12	4
Left Middle Frontal Gyrus (46)		–38	30	12
Right Inferior Parietal Lobule (40)	8,720	38	–48	46
Right Precuneus (7)		18	–68	42
Right Supramarginal Gyrus (40)		48	–44	34
Right Cuneus (7)		20	–74	32
Right Cuneus (19)		28	–76	26
Right Angular Gyrus (39)		34	–60	38
Right Superior Temporal Gyrus (13)		52	–44	20
Left Precuneus (19)	4,160	–28	–62	38
Left Precuneus (7)		–20	–70	42
Left Precuneus (7)		–18	–64	48
Left Precuneus (7)		–12	–72	34
Right Middle Frontal Gyrus (6)	3,056	24	–6	52
Left Inferior Parietal Lobule (40)	2,408	–44	–44	40
Left Lentiform Nucleus Putamen	912	–18	8	4
Left Caudate Body		–16	2	14
Left Thalamus Mammillary Body	520	–12	–20	0
Right Thalamus	456	12	–10	14
Right Superior Frontal Gyrus (10)	376	34	50	20
Right Middle Frontal Gyrus (10)		30	42	18
Right Inferior Frontal Gyrus (10)	304	38	46	4
Right Inferior Occipital Gyrus (19)	232	40	–72	0
Left Inferior Occipital Gyrus (19)	216	–38	–74	0
Right Lingual Gyrus (18)	200	10	–82	–4
Left Parahippocampal Gyrus (19)	192	–18	–52	–6
Right Thalamus	176	6	–18	0
Left Cerebellar Declive	160	–34	–62	–20
Left Middle Frontal Gyrus (10)	160	–34	46	18
Right Superior Frontal Gyrus (9)	160	22	40	34

Table 6 Brain regions (Brodmann areas in parentheses) with significant activation within healthy adults within the working memory

Brain Region (BA)	Volume (mm^3)	Maxima		
		x	*y*	*z*
Right Middle Frontal Gyrus (9)	103,712	38	30	28
Left Superior Frontal Gyrus (6)		–2	6	52
Right Frontal Lobe Sub-Gyral (6)		26	2	54
Left Cingulate Gyrus (32)		0	16	40
Right Insula (13)		32	20	6
Left Inferior Frontal Gyrus (9)		–44	6	26
Left Precentral Gyrus (6)		–46	0	36
Left Insula (13)		–32	18	6
Right Inferior Frontal Gyrus (9)		44	6	32
Left Middle Frontal Gyrus (6)		–26	–4	50
Left Middle Frontal Gyrus (9)		–40	28	28
Left Middle Frontal Gyrus (10)		–36	42	20
Left Middle Frontal Gyrus (46)		–42	16	24
Left Lentiform Nucleus Putamen		–18	–4	12
Right Inferior Frontal Gyrus (47)		44	18	–2
Left Precentral Gyrus (44)		–48	14	8
Left Lentiform Nucleus Putamen		–22	8	4
Left Middle Frontal Gyrus (10)		–28	54	4
Left Cingulate Gyrus (24)		0	–2	36
Left Precentral Gyrus (6)		–60	2	14
Right Inferior Parietal Lobule (40)	8,896	40	–50	40
Right Cuneus (19)		28	–76	30
Right Precuneus (7)	8,152	10	–66	46
Left Cerebellar Declive	3,320	–36	–58	–20
Left Fusiform Gyrus (37)		–44	–52	–14
Left Cerebellar Declive		–38	–70	–14
Right Cerebellar Tuber	3,056	34	–60	–30
Left Thalamus	864	–4	–20	12
Right Thalamus		8	–14	4
Left Inferior Parietal Lobule (40)	728	–38	–50	40
Right Cerebellar Declive	448	2	–64	–22
Right Caudate Caudate Body	264	16	–6	20

these systems may be segregated, they may be differentially engaged during executive functions. A study of the degree to which systematic differences exist in the engagement of discrete elements (regions or subnetworks) of the cognitive control networks across different executive function domains is beyond the resolution of this meta-analysis, and our understanding of this issue will be informed by future experimental studies, particularly those that include direct measures of intraregion connectivity or network dynamics across task demands.

While the use of quantitative meta-analytic methods allowed us to examine executive functions across a variety of tasks and domains within the largest sample of healthy adults to date, it is important to recognize that these findings are limited by the quality of the data available in the extant literature. Activation likelihood estimation requires the reporting of imaging data in three-dimensional coordinates in a standard brain space. Therefore, this analysis did not include studies in which such data were not reported for relevant contrasts (e.g., a within-subjects contrast related to the primary effect of interest in healthy controls), analyses that focused on particular regions of interest, or studies that reported negative findings, as the ALE method does not allow for the modeling of null results (Li, Chan, McAlonan, & Gong, 2010). Furthermore, the lack of appropriate contrasts, such as contrasting an active task with rest or fixation, reduced the number of studies available for inclusion within each domain. However, the use of an active control

Table 7 Preliminary data for brain regions (Brodmann areas in parentheses) with significant activation within healthy adults for tasks within the initiation domain

Brain Region (BA)	Volume (mm^3)	Maxima		
		x	*y*	*z*
Left Cingulate Gyrus (32)	6,064	–6	18	32
Right Cingulate Gyrus (32)		4	14	38
Right Cingulate Gyrus (32)		2	22	30
Left Middle Frontal Gyrus (46)	4,160	–42	26	20
Left Inferior Frontal Gyrus (46)		–42	38	12
Left Inferior Frontal Gyrus (45)		–50	20	4
Left Precentral Gyrus (44)		–46	12	8
Left Middle Temporal Gyrus (21)	904	–60	–58	0
Right Cerebellar Declive	632	22	–76	–16
Right Cerebellar Culmen	584	6	–36	2
Left Cerebellar Declive	504	–34	–64	–22
Right Occipital Lobe Lingual Gyrus (17)	472	2	–84	6
Right Middle Frontal Gyrus (46)	384	42	32	18
Left Superior Temporal Gyrus (22)	352	–60	–56	18
Right Claustrum	344	26	20	2
Right Middle Frontal Gyrus (11)	312	26	38	–6
Left Lentiform Nucleus Putamen	216	–20	10	4
Right Caudate Body	160	14	4	14
Right Medial Frontal Gyrus (6)	128	2	36	34
Left Inferior Frontal Gyrus (45)	120	–36	24	4

condition is essential in order to isolate the cognitive process of interest in subtraction contrasts (Stark & Squire, 2001). Our approach to this analysis integrated findings from both fMRI and O^{15} PET studies, and the ALE method does not account for the potential influence of the different physiological signals associated with these two methods. Additionally, this method does not account for differences in behavioral performance across tasks or the influence of demographic factors, although the sample was restricted to studies that examined a specific age range (18–60 years). While all available studies within the BrainMap database were considered for this analysis, studies that were not included in the database at the time of the analysis have been omitted. Furthermore, this meta-analytic method does not allow for the weighting of results on the basis of levels of statistical significance or the numbers of activation foci that may have been reported by some studies within this investigation (Li, Chan, McAlonan, & Gong, 2010). Although Gaussian blurring of the coordinates will have tended to remove per-study bias of the peak activation localizations, noise within the data might have influenced the study results (M. G. Berman et al., 2010). Finally, our definition of executive functions was based on a traditional view that is often used in cognitive or neuropsychological research (Lezak, 1995; Luria, 1970; Shallice, 1988), and the use of other definitions might have altered the domains examined.

In conclusion, the present study used the meta-analysis of a very large number of published fMRI data sets to examine whether traditional taxonomies of executive functions purporting discrete modular cognitive domains are supported by a superordinate cognitive control system that is engaged during the performance of a range of executive function tasks. Our results suggest that a frontal–cingulate–parietal–subcortical cognitive control network is consistently recruited across a range of traditional executive function tasks. Further research investigating the contributions of modular (e.g., prefrontal) versus shared elements (e.g., frontal–parietal connectivity) of the cognitive control network will inform our understanding of common and unique patterns of impairment in traditional executive functions that are often associated with various brain disorders. Novel approaches to investigating the function of different component systems using single methodologies (e.g., resting state; Deshpande, Santhanam, & Hu, 2011) or combined methodologies (e.g., EEG and fMRI; Debener et al., 2005) have the potential to elucidated the complex brain dynamics underlying cognitive control. Further studies will be needed to make explicit the precise functional contributions of each individual element of the cognitive control network, as well as to understand the complex interactions between network nodes to support coordinated, goal-directed behavior. Through increased understanding of the function of modular components within this network, along with their anatomical connections and functional interactions, we will be able to more effectively investigate the mechanisms by which aberrant behavior or clinical symptoms may result from dysfunction in individual regions or in their connectivity within the broader network (Menon, 2011). Additional research on the relationship between various imaging modalities (e.g., resting state, task-related fMRI, or diffusion tensor imaging) will also help us to uncover ways in which discrete brain systems interact to support complex cognition and behavior.

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