Neural substrates of the executive function construct, age-related changes, and task materials in adolescents and adults: ALE meta-analyses of 408 fMRI studies

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CONFLICT OF INTEREST

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available from the corresponding author (Zheng Zhang, zzhang86@utexas.edu) upon reasonable request.

Research highlights

- The multiple-demand network underpins EF processes across adolescence and adulthood.
- Only working memory was found separable from common EF in adolescents.
- Inhibition, switching, and working memory were found separable from common EF in adults.
- Inhibition and working memory showed both domain generality and domain specificity, whereas switching showed only domain-generality.
- Findings of switching in adolescents should be treated with caution and those analyses may be exploratory due to limited data available on switching tasks.

Abstract

To explore the neural substrates of executive function (EF), we conducted an activation likelihood estimation (ALE) meta-analysis of 408 functional magnetic resonance imaging studies (9,639 participants, 7,587 activation foci, 518 experimental contrasts) covering three fundamental EF subcomponents: inhibition, switching, and working memory. Our results found that activation common to all three EF subcomponents converged in the multiple-demand network across adolescence and adulthood. The function of EF with the multiple-demand network involved, especially for the prefrontal cortex and the parietal regions, could not be mature until adulthood. In adolescents, only working memory could be separable from common EF, whereas in adults, the three EF subcomponents could be separable from common EF. However, findings of switching in adolescents should be treated with substantial caution and may be exploratory due to limited data available on switching tasks. For task materials, inhibition and working memory showed both domain generality and domain specificity, undergirded by the multiple-demand network, as well as different brain regions in response to verbal and nonverbal task materials, respectively. In contrast, switching showed only domain generality with no activation specialized for either verbal or nonverbal task materials. These findings, taken together, support and contribute to the unitary–diverse nature of EF such that EF should be interpreted in an integrative model that relies on the integration of the EF construct, development, and task materials.

Keywords: Executive function, Integrative model, Development, Domain-general, Domain-specific, ALE meta-analysis

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1. INTRODUCTION

Executive function (EF) refers to a set of cognitive processes involved in general-purpose mechanisms for executing goal-directed actions (Friedman & Miyake, 2017). EF comprises three core and commonly studied subcomponents (Miyake & Friedman, 2012): *inhibition* (resistance of dominant, automatic, or prepotent actions, including behavioral inhibition [response inhibition or self-control] and interference control [selective attention and cognitive inhibition]; Diamond, 2013); *switching* (flexibly shifting between tasks or mental sets; Dajani & Uddin, 2015); and *working memory* (simultaneous storage and manipulation of information in the mind; Baddeley, 2010). EF is essential for the regulation of human cognition and behavior (Calderon & Bellinger, 2015). Deficits in EF are associated with various neurological/physical disorders and developmental delays (Ilieva et al., 2018). Given the importance of EF, the present meta-analyses of functional magnetic resonance imaging (fMRI) studies are intended to uncover the neural mechanisms underlying EF in terms of its construct, development, and task materials. In the following sections, we specifically review and discuss theories, evidence, and potential explanations in debates on EF.

1.1 The EF construct

The widely accepted integrative model suggests that EF is both unitary and diverse (Friedman & Miyake, 2017). While common EF represents a common underlying ability/mechanism to maintain task goals that is necessary for inhibition, switching, and working memory, the three subcomponents capture construct-specific EF processes beyond what is accounted for by common EF and are argued intra-related and inter-dependent from each other

(Friedman et al., 2011). Early studies have linked EF to frontal functioning (Jurado et al., 2007; Lewis et al., 2004). Recently, evidence has converged to the essential involvement of the multiple-demand network in EF (Assem et al., 2020; Müller et al., 2015; Yao et al., 2020). This network refers to a common brain pattern responding to various task demands, consisting of brain regions in and around the inferior frontal sulcus and intraparietal sulcus, as well as the insula and adjacent frontal operculum, pre-supplementary motor area, and anterior cingulate cortex (Duncan, 2010; Camilleri et al., 2018). However, there are still disagreements on whether there is a shared cognitive mechanism (common EF) across different subcomponents (e.g., Baggetta & Alexander, 2016; Diamond, 2013) and research has often yielded contradictory findings of brain patterns for common EF and the three subcomponents.

1.1.1 Common EF

Given the integrative model, while some meta-analyses have revealed shared brain activation across EF subcomponents (Mckenna et al., 2017; Niendam et al., 2012), others have not (Lenartowicz et al., 2010; Stuss & Alexander, 2007). These contradictory findings may be due to differences in the ages of samples (Miyake & Friedman, 2012). Even for the meta-analyses that have identified common EF, brain patterns have varied. For example, the multiple-demand network has been found to serve the function of common EF (Mckenna et al., 2017; Niendam et al., 2012). However, Alvarez and Emony (2006) also found that some regions outside this network mediated common EF. The inconsistency may be a result of different sets of EF subcomponents involved in the meta-analyses. For example, Niendam et al. (2012) used inhibition, updating, and switching to assess EF, whereas Alvarez and Emony (2006) included flexibility, fluency, and inhibition to represent EF.

1.1.2 EF subcomponents

It remains unclear which subcomponent can be considered as truly separable from common EF. Based on our review, only one neuroimaging meta-analysis (McKenna et al., 2017) has examined activation specialized for each subcomponent compared with common EF. The results identified common EF across inhibition, switching, and working memory, and found that switching and working memory could be separable from common EF but inhibition could not. However, Mckenna et al. only focused on young individuals (6–18 years), limiting the understanding of the EF construct across development.

Additionally, findings of EF meta-analyses that have focused on specific subcomponents are conflicting. Simmonds et al. (2008) emphasized the role of the pre-supplementary motor area in inhibition. However, Criaud and Boulinguez (2013) argued that the pre-supplementary motor area was driven by the engagement of high attentional or working memory resources but not inhibition. Contradictory findings have also been reported for switching (Buchsbaum et al., 2005; McKenna et al., 2017) and working memory (Owen et al., 2005; Rottschy et al., 2012).

1.2 Development

The integrative model has been confirmed by many studies across different age groups (Ito et al., 2015; Vaughan & Giovanello, 2010). Such a unitary and diverse pattern of EF could vary with age. In the early developmental stage (before 5 years), EF may be indistinguishable (Wiebe et al., 2011). Over 5 years, EF may be overlapping but partially distinguishable (Brydges et al. 2014). During adolescence (over 10 years), different EF subcomponents, although share common variance, may be separable from one another to some extent (St Clair-Thompson & Gathercole, 2006). In adulthood (over 18 years), studies have generally identified common EF and each of the three subcomponents (Miyake & Friedman, 2012; Zelazo et al., 2004). Furthermore, the developmental trajectories of EF subcomponents would be relatively different such that inhibition was improved throughout adolescence, switching was seen to develop in late adolescence, while working memory continued to develop into young adulthood (Huizinga et al., 2006; Hunter et al., 2012). Such age-related changes in the EF construct were also revealed in a behavioral meta-analysis (Karr et al., 2018).

However, findings of the developmental pattern of EF across neuroimaging meta-analyses are inconsistent. Mckenna et al. (2017) identified common EF and separable switching and working memory in children and adolescents, whereas Houdé et al. (2010) did not find such evidence. In adults, Lenartowicz et al. (2010) discriminated brain activation for separable inhibition, switching, and working memory but did not identify shared activation for common EF. Whereas Niendam et al. (2012) revealed shared activation for common EF and different activation specialized for inhibition, switching, working memory, and initiation among adults.

There is a lack of neuroimaging meta-analyses investigating age-related changes in each subcomponent since many meta-analyses have combined different age groups into a single sample (Cortese et al., 2013; Hart et al., 2013). Nonetheless, findings from empirical studies may indicate differences in development for each subcomponent. For inhibition, young individuals (aged 8-20 years) showed higher dorsolateral prefrontal activation (Durston et al., 2006), whereas adults showed higher ventral prefrontal activation (Lamp et al., 2016). For switching, Rubia et al. (2006) found age-related increases in the anterior cingulate cortex and decreases in the dorsolateral prefrontal cortex. For working memory, Ciesielski et al. (2006) revealed greater activation in the inferior frontal gyrus and inferior temporal gyrus in adults, but greater activation in the premotor cortex, cerebellum, and insula in adolescents.

1.3 Task materials

EF has been proposed as contributing to human learning and academic performance (Cragg & Gilmore, 2014; Peng & Kievit, 2020). Within this context, is the EF construct considered as a domain-general process (a general capacity) independent of different types of task materials (Baddeley, 2010)? Or does the EF construct represent a domain-specific process such that EF in a specific type of task material is markedly distinct from what is seen in other task materials (verbal vs. nonverbal; Demoulin & Kolinsky, 2016)?

The debate on domain-generality versus domain-specificity has been mainly discussed within the framework of working memory (Peng et al., 2012, 2018). Some researchers have indicated the domain-specificity such that verbal working memory tasks and spatial working memory tasks loaded onto distinct factors (Karbach et al., 2015; Oberauer et al., 2008). In contrast, Perone et al. (2019) studied working memory using a dynamic neural field model, which consisted of frontal and posterior regions. The frontal regions (e.g., dorsolateral prefrontal cortex) represented a general working memory process independent of different task materials, whereas the posterior regions (e.g., parietal lobule) were responsible for generating responses based on different task materials. The model appeared to indicate both domain-generality and domain-specificity in working memory, in line with neuroimaging meta-analyses (Owen et al., 2005; Nee et al., 2012)

A few empirical studies have explored the domain nature of inhibition and switching. For example, the left inferior frontal gyrus was more associated with verbal inhibition tasks, whereas the right inferior frontal gyrus was more associated with nonverbal inhibition tasks (Davey et al., 2015). fMRI results showed left-lateralization of activation in frontal and parietal regions during verbal switching tasks, whereas activation in bilateral frontal and parietal regions during nonverbal switching tasks (Anderson et al., 2018; Vallesi et al., 2015). However, there is no neuroimaging meta-analysis exploring whether inhibition and switching could be affected by task materials.

1.4 Research aims

The purpose of the present meta-analysis is to explore the neural substrates underlying the EF construct with age and task materials effects. There are three questions: (1) Is EF a unitary construct or a set of independent subcomponents? That is, to what degree does each subcomponent differ from common EF? (2) What is the brain pattern for each subcomponent within adolescents and adults, respectively? (3) What are the different brain patterns between verbal and nonverbal domains for each subcomponent? We hypothesize that shared activation across the three subcomponents could be revealed to represent common EF and unique activation could be specialized for each subcomponent. Within adolescents, not all subcomponents are separable from common EF, while within adults the three subcomponents may be separable from common EF. Inhibition and switching could be domain-specific, while working memory could be both domain-general and domain-specific.

2. METHOD

2.1 Literature search and selection criteria

Studies were identified in three ways. First, a computer search of PsycArticles, PsycInfo, MedLine, and ERIC databases was conducted with the search terms ([“working memory” OR “inhibit*” OR “switch*” OR “flexib*” OR "shift*" OR “updat*” OR “refresh* OR "execut*"”] AND [“fMRI” OR “functional magnetic resonance imaging”]). Second, we hand searched citations in prior relevant reviews. Finally, we completed forward and backward searches by reviewing the reference lists of the included studies and searching all studies that cited the included studies.

We conducted the original search from January 1993 through December 2017, which identified 27,023 studies (PsycArticles 6,481; PsycInfo 9,626; ERIC 215; MedLine 10,701; other resources 3,624). Then, we conducted the second search from January 2018 through March 2020 to update our dataset, which yielded 6,174 studies (PsycArticles 1,368; PsycInfo 1,984; ERIC 7; MedLine 2,815; other resources 1,061). A total of 37,882 studies were identified. After excluding 594 duplicate studies, 37,288 studies remained. Of these, 34,063 studies were excluded because after preliminary screening (reviewing the titles and abstracts) these studies did not meet the inclusion criteria. The remaining 3,225 studies were further screened (reviewing the full text) according to the following criteria:

1. Studies using fMRI to explore human brain activation were included. Studies using other techniques (e.g., EEG, DTI) were excluded. Single-subject studies were excluded.
2. Studies reporting activation data resulting from subtractions between target conditions and task baseline conditions (lower cognitive load and sensorimotor conditions) were included. Data were excluded if resulting from: (1) subtractions between target and resting-state conditions as these data involve the influence of low-level perceptual or motor processes in the results of meta-analyses (Kim et al., 2012); (2) conjunction and common analyses as they do reduce the inference space to only regions of the contrasts involved in those analyses (Müller et al., 2018); (3) correlations between activation and predictors (e.g., IQ scores, reaction time) because these data do not purely reflect the critical processes of EF; (4) functional connectivity, independent component, and principal component analyses. Deactivation data were excluded.
3. Studies reporting data from typically developing participants were included. Data from participants with disorders (e.g., ADHD, ASD) were excluded. When studies with

patients had a healthy control group, data from the control group were included if separable. Data related to sleep deprivation, after-training, and pharmacological manipulation were excluded.

4. Studies reporting data from whole-brain analyses as coordinates in standard reference space (Talairach or MNI) were included. Region of interest (ROI) and small volume corrected (SVC) analyses would inflate significance for the regions that come from overrepresented in ROI/SVC analyses and these data were excluded. SVC analyses should potentially be included if peaks in the regions were statistically thresholded as in the rest of the brain (Müller et al., 2018).
5. Studies including samples aged less than 10 years or greater than 40 years were excluded.

A total of 408 studies were identified as eligible for inclusion in our meta-analyses (Table 1). Figure 1 shows the PRISMA flow chart for the literature screening process (Liberati et al., 2009). All studies measured "cool" EF, which operates in more affectively neutral contexts (a task that "does not involve obvious rewards or punishers"), unlike "hot" EF, which operates in "motivationally and emotionally significant high-stakes situations" (Zelazo & Carlson, 2012, p. 355). The 408 studies included data from 9,629 participants and reported 7,587 activation foci in 518 experimental contrasts.

2.2 Coding procedure

A coding manual on study information was created, including authors, publication date, demographics, EF types, tasks, experimental contrasts, and stimulus materials (see Table S1). All studies were coded by the first author and a trained graduate student, separately. The interrater reliability averaged across the characteristics was .92. Any coding inconsistency was resolved through discussion or by referring to the original studies.

2.3 Missing data

Not all studies reported complete information on the characteristics of interest. To obtain the missing information, the studies' researchers were contacted by e-mail. Most of the researchers responded and provided the missing data.

2.4 Coordinates grouping

Coordinates were grouped into different meta-analyses: (1) common EF (convergence across inhibition, switching, and working memory); (2) each subcomponent (convergence tapping a specific subcomponent). These meta-analyses were further separately sorted into: (1) an adolescent group (greater than or equal to 10 years and less than or equal to 18 years), an adult group greater than 18 years and less than or equal to 40 years), and a whole sample group (including the adolescent and the adult groups). We used a cut-off of 18 years for separating age groups and excluded samples aged less than 10 years and greater than 40 years because both behavioral and neuroimaging studies suggest that the three subcomponents improve from childhood to young adulthood and decline in older age (Andre et al., 2016; Leiva et al., 2016); (2) verbal and nonverbal groups. Verbal domain included EF tasks that required words, letters, digits, and sentences. Nonverbal domain included EF tasks that required manipulation of dots, objects, shapes, and pictures.

The numbers of contrasts, foci, and participants included in each group are summarized in Table 2. Data from a particular study could be excluded from one meta-analysis due to inseparable data. For example, if data from adolescents and adults in the same study were not separable, we only included those data in the whole sample group but not in the two age groups. A single study may have multiple contrasts of the same type. To minimize within-experiment effects, those contrasts were combined into a single contrast to represent the study unless they were resulted from nonoverlapping samples (Turkeltaub et al., 2012).

2.5 Activation likelihood estimation meta-analyses

To identify the orientation (e.g., RPI/LPI) of coordinates, we visually inspected the spheres convolved from coordinates and compared with figures in the study (Tervo-Clemmens et al., 2020). Twenty-seven studies reported coordinates as RPI and 381 studies reported coordinates as LPI. Coordinates reported as RPI were transformed into LPI. Then, coordinates reported in Talairach space were transformed into MNI according to the Lancaster transform (Lancaster et al., 2007).

We performed meta-analyses with BrainMap GingerALE software (version 3.0.2; Eickhoff et al., 2012). ALE is a coordinate-based meta-analysis technique used for the quantitative evaluation of spatial convergence. Convergence is interpreted as activation in regions that are consistently found across studies. First, foci are pooled from each study and converted to a standardized coordinate space. The foci are modeled as Gaussians (probability values) and the widths of those Gaussians are calculated based on the number of participants in each study to adjust spatial uncertainty. If samples of several studies are overlapped, a focus may have several Gaussians associated with those studies. ALE chooses the Gaussian having the maximum probability value in the focus among those studies. That is, ALE combines those studies into a single experiment to minimize within-group effects (Turkeltaub et al., 2012). All chosen Gaussians form an ALE map. To differentiate true from random brain effects, ALE scores are then compared with a null distribution showing random effects among all modeled Gaussians. The *p* value of an ALE score is determined by the proportion of values higher than the null distribution, resulting in a statistical ALE map.

Contrast meta-analyses include both conjunction and comparison analyses. Conjunction analyses reveal significant shared activation between two thresholded ALE maps (resulting from individual meta-analysis) using the voxel-wise minimum value of the two maps (Cieslik et al., 2015). Comparison analyses reveal significant differences in convergence between two thresholded ALE maps by computing the voxel-wise differences between them (Langner & Eickhoff, 2013). To determine a null distribution of differences, ALE creates simulated data by pooling all experiments from the two maps (Eickhoff et al., 2011). The pooled experiments are then randomly dividing into two new datasets of the same sample size as the original datasets of experiments. Next, ALE score differences between the two new datasets are subtracted from each other. With permutations (e.g., 10,000), an empirical null distribution of ALE score differences between the two conditions is created. The "true" ALE score differences between the two conditions are then compared with this null distribution. Finally, a voxel-wise *p* value image is created and converted to *Z* scores to show the significance.

When comparing two individual meta-analysis maps (e.g., A and B) associated with different cognitive processes (or different age groups), a difference in convergence is found in a brain region in the A vs. B contrast meta-analysis map. This result indicates that there is a higher frequency of observing activation in this region for A than for B (Rottschy et al., 2012), even though both A and B individual meta-analysis maps could show significantly higher than chance convergence in this region.

2.5.1 Individual ALE meta-analyses

Individual meta-analyses were conducted for common EF and each subcomponent within the adolescent group, the adult group, and the whole sample group, separately. These analyses were also conducted separately for each subcomponent, given a specific task material (verbal or nonverbal). A permutation testing with 10,000 iterations was conducted. All *p* values were cut off at $p < .05$ with a cluster-level family-wise error (FWE) correction (cluster-forming threshold at voxel level, $p < .001$) to correct for multiple comparisons and avoid false positives (Eickhoff et al., 2016).

2.5.2 Contrast ALE meta-analyses

Differences in convergence between each subcomponent and common EF were examined to reveal brain regions specialized for each subcomponent. Possibly, the same study might be included in the individual meta-analyses for both common EF and a specific EF subcomponent, which would introduce a bias toward significant conjunction. This is solved by comparing a specific subcomponent to other subcomponents combined. For example, to reveal inhibition-specific activation, the ALE map for inhibition was compared with that for “common EF” (switching and working memory). These analyses were conducted for each subcomponent in the whole-sample group, the adolescent group, and the adult group, separately.

Then, contrast meta-analyses were conducted to reveal differences in convergence between the two age groups for common EF and each subcomponent, separately, to identify age-related changes. Next, contrast meta-analyses between verbal and nonverbal domains were examined for each subcomponent to reveal task material effects.

For all contrast analyses, the threshold was set to uncorrected $p < .01$ (10,000 permutations, 400 mm^3 minimum volume; Arsalidou et al., 2020).

3. RESULTS

3.1 Construct (whole sample)

3.1.1 Individual ALE meta-analyses

Individual ALE meta-analyses for common EF and each subcomponent both revealed convergence in the multiple-demand network. Moreover, convergence was also found in: (1) the bilateral precuneus, bilateral supramarginal gyri, left inferior occipital gyrus, bilateral thalamus, and bilateral caudate for the common EF analysis (572 contrasts, 7,587 foci, 9,639 participants); (2) the bilateral hemispheres including the precuneus, supramarginal gyrus, middle occipital gyrus, and putamen, as well as the right inferior occipital gyrus, left caudate, and right thalamus for the inhibition analysis (253 contrasts, 3,788 foci, 6,081 participants); (3) the bilateral precuneus, left thalamus, left putamen, and left caudate for the switching analysis (133 contrasts, 1,675 foci, 3,284 participants); (4) the bilateral precuneus, left inferior temporal gyrus, left caudate, and bilateral cerebellar hemispheres for the working memory analysis (132 contrasts, 2,124 foci, 2,304 participants; Tables S1-2).

3.1.2 Contrast meta-analyses

Inhibition vs. common EF (switching and working memory) revealed differences in convergence in part of the multiple-demand network, right inferior occipital gyrus, left middle occipital gyrus, right middle/superior temporal gyri, and left supramarginal gyrus (Table S3).

Switching vs. common EF (inhibition and working memory) revealed differences in convergence in the left superior frontal gyrus, right precuneus, and left superior parietal lobule (Table S3).

Working memory vs. common EF (inhibition and switching) revealed differences in convergence in part of the multiple-demand network and bilateral cerebellum (Table S3).

3.2 Development

3.2.1 Individual ALE meta-analyses

Common EF. For both age groups, common EF showed convergence in the multiple-demand network. Moreover, in adolescents (62 contrasts, 762 foci, 1,403 participants), convergence was found in the right precuneus, left caudate, and bilateral thalamus; in adults (133 contrasts, 1,675 foci, 3,284 participants), convergence was found in the left inferior occipital gyrus, bilateral precuneus, bilateral thalamus, and bilateral caudate (Table S1).

Inhibition. For both age groups, inhibition showed convergence in the multiple-demand network. Moreover, in adolescents (33 contrasts, 408 foci, 1,075 participants), convergence was found in the right thalamus; in adults (219 contrasts, 3,387 foci, 4,726 participants), convergence was found in the bilateral precuneus, bilateral supramarginal gyri, left inferior occipital gyrus, right thalamus, left fusiform, right thalamus, bilateral caudate, and right putamen (Figure 2; Table S2).

Switching. In adolescents (6 contrasts, 58 foci, 296 participants), switching showed convergence in the left medial frontal gyrus. In adults (126 contrasts, 1,584 foci, 2,785 participants)**,** convergence was found in the multiple-demand network, bilateral precuneus, left thalamus, left caudate, and left putamen (Figure 2; Table S2).

Working memory. For both age groups, working memory showed convergence in the multiple-demand network, left caudate, and the cerebellum (adolescents: 23 contrasts, 296 foci, 449 participants; adults: 109 contrasts, 1,828 foci, 1,855 participants; Figure 2; Table S2).

3.2.2 Contrast meta-analyses for each subcomponent compared with common EF

Inhibition. In adolescents, differences in convergence (inhibition vs. common EF [switching and working memory]) were observed in pars triangularis of the right inferior frontal gyrus and precentral gyrus; in adults, differences in convergence were observed in part of the multiple-demand network, the bilateral supramarginal gyri, left middle occipital gyrus, and right superior temporal gyrus (Figure 3; Table S3).

Switching. In adolescents, no difference in convergence (switching vs. common EF [inhibition and working memory]) was observed. In adults, differences in convergence were observed in the left superior frontal gyrus, left inferior and superior parietal lobule, and left precuneus (Figure 3; Table S3).

Working memory. For both age groups, differences in convergence (working memory vs. common EF [inhibition and switching]) were observed in the multiple-demand network and the cerebellum (Figure 3; Table S3).

3.2.3 Contrast meta-analyses between adolescents and adults

By comparing common EF and each subcomponent between the two age groups, differences in convergence were observed in some of the frontal regions for adolescents, whereas in both frontal and parietal regions for adults. In addition, for working memory, adolescents showed differences in convergence in the left cerebellum compared with adults (Figure 4; Table S4).

3.3 Task materials

3.3.1 Individual ALE meta-analyses

Verbal inhibition (115 contrasts, 1,740 foci, 2,469 participants) and nonverbal inhibition (138 contrasts, 2,048 foci, 3,284 participants) both showed convergence in the multiple-demand network. Moreover, verbal inhibition showed convergence in the bilateral supramarginal gyri and left precuneus; nonverbal inhibition showed convergence in the right supramarginal gyrus, left inferior occipital gyrus, left inferior temporal gyrus, bilateral precuneus, left caudate, bilateral putamen, and right thalamus (Table S5).

Verbal switching (46 contrasts, 626 foci, 1,239 participants) and nonverbal switching (87 contrasts, 1,049 foci, 2,045 participants) both showed convergence in the multiple-demand network and left precuneus (Table S5).

Verbal working memory (71 contrasts, 1,244 foci, 1,229 participants) and nonverbal working memory (60 contrasts, 867 foci, 1,049 participants) both showed convergence in the multiple-demand network and bilateral cerebellum (Table S5).

3.3.2 Contrast meta-analyses

Conjunction analyses. Convergence between verbal and nonverbal domains for each subcomponent was commonly found in the multiple-demand network (Table S6).

Comparison analyses. By comparing inhibition between the two domains, verbal inhibition showed differences in convergence in pars triangularis of the left inferior frontal gyrus, left middle and medial frontal gyri, and left inferior and superior parietal lobule. Nonverbal inhibition showed differences in convergence in the bilateral precuneus and right middle and superior frontal gyri (Figure 5; Table S7).

For switching, no difference in convergence was revealed for either verbal or nonverbal switching (Figure 5; Table S7).

Verbal working memory showed differences in convergence in pars opercularis of the bilateral inferior frontal gyri, pars triangularis of the right inferior frontal gyrus, right inferior parietal lobule, left thalamus, and left putamen. Nonverbal working memory showed differences in convergence in the bilateral precuneus and left middle frontal gyrus (Figure 5; Table S7).

3.4 Control meta-analyses

Control meta-analyses were conducted to verify results from contrast meta-analyses by controlling for unbalanced numbers of foci and experimental contrasts in those contrast analyses

(McKenna et al., 2017). For example, there were 62 experimental contrasts (762 foci, 1,403 participants) in the adolescent dataset of common EF but 454 experimental contrasts (6,799 foci, 8,236 participants) in the adult dataset of common EF. To match the lower number of foci (762) and experimental contrasts (62) in the adolescent dataset, the adult dataset was randomly separated into seven subgroups with approximately 854 foci and 57 experimental contrasts (Table S10). To reduce bias, each subgroup of adults for common EF contained different studies from the original adult dataset in common EF. Then, the adolescent dataset of common EF was compared with each of the seven subgroups of adults.

Control analyses were conducted if the numbers of foci and experimental contrasts in contrast analyses were unbalanced and the numbers of those experimental contrasts were greater than 17 to have sufficient power (Eickhoff et al., 2016): (1) switching vs. common EF and working memory vs. common EF in the whole group and the adult group; (2) adolescents vs. adults for common EF, inhibition, and working memory; (3) verbal switching vs. nonverbal switching. Results revealed: (1) switching-specific activation in some of the frontal and parietal regions, and working memory-specific activation in the cerebellum and part of the multiple-demand network in the whole group and the adult group; (2) for common EF, inhibition, and working memory, adolescents were more associated with some of the frontal regions, while adults were more associated with the prefrontal cortex and parietal regions; (3) only one difference in convergence was found in the superior parietal lobule for nonverbal switching compared with verbal switching (Tables S8-12). These results from control analyses were consistent with contrast meta-analyses and perhaps provided verification for contrast meta-analyses.

3.5 Contributions of the included studies to specific brain regional effects

Post-hoc analyses were conducted to provide more detailed information about ALE effects (Müller et al., 2018). In the Supplementary Material, we present the number of studies that contributed to specific regional effects. For the individual meta-analyses, half of the studies or more included in a specific analysis contributed to the effect in a region. Relatively fewer studies contributed to the contrast meta-analyses, where half of the included studies or less in a specific analysis contributed to the effect in a cluster. Overall, it was relatively unlikely that the results were driven by only one or two experimental contrasts, given the large number of experiments included in the present meta-analyses (Eickhoff et al., 2012).

4. DISCUSSION

4.1 The EF construct

4.1.1 Common EF

Convergence for common EF was found in the multiple-demand network, especially the insula, inferior frontal gyri, and inferior parietal lobule. Convergence in this network was also revealed across the three subcomponents. The multiple-demand network has been reported to support common EF to actively maintain task goals and goal-related information and use this information to effectively bias ongoing processing (Assem et al., 2020; Spreng et al., 2010). This goal-oriented cognition is assumed to contribute to general EF processes (Davey et al., 2016). We suggest that the multiple-demand network constitutes the pivotal construct for all EF processes.

The insula is known for its role in mediating bottom-up stimulus-driven processes and biasing of sensory input by top-down attentional control. This dynamic process can sift through different incoming sensory stimuli and adjust the gain for task-relevant stimuli central to attention (Menon & Uddin, 2010). The inferior frontal gyrus and inferior parietal lobule are also involved in top-down attentional control to behaviorally select relevant stimuli and suppress task-irrelevant information during EF tasks (Bowling et al., 2020; Liu et al., 2020). Therefore, we suggest that the multiple-demand network is associated with executive control of top-down attention to subserve all EF processes.

4.1.2 The Three EF subcomponents

Based on the individual meta-analyses, each subcomponent showed convergence in the multiple-demand network, in line with previous studies reporting that the network subserves all EF processes (Müller et al., 2015; Yao et al., 2020). Compared with common EF, each of the three subcomponents showed differences in convergence in the multiple-demand network. However, differences (magnitudes and variability of activation) within this network do not necessarily yield functional dissociations among different EF subcomponents because those differences could not detect the specific activation of an EF subcomponent (Daws et al., 2020; Tsuchida & Fellows, 2013). Instead, those differences may imply that an EF subcomponent is more sensitive to or requires more cognitive demands on the multiple-demand network, but the network still supports a wide range of cognitive processes. Thus, differences in convergence in the network may not appear to be specialized for an EF subcomponent.

Inhibition. Compared with common EF, in addition to regions within the multiple-demand network, inhibition was more associated with the right superior and middle temporal gyri and right inferior occipital gyrus. Previous studies have indicated that the inferior occipital gyrus is associated with visual recognition of objects (Coggan et al., 2019; Ludersdorfer et al., 2019). The engagement of the inferior occipital gyrus in our findings indicates the encoding of task-relevant visual information to modulate inhibition control. The temporal regions have been correlated with successful performance on inhibition tasks (Antons et al., 2019). Evidence has implied that the temporal regions underlie the long-term storage of information and the short-term retention and integration of new recalled information (Owen, 2000; Takahashi et al., 2007). Our findings may suggest that the superior and middle temporal gyri serve to rehearse or hold task-relevant information in mind to enhance performance during inhibition tasks. Taken together, the occipital and temporal regions may be specialized for inhibition.

Switching. Compared with common EF, switching showed differences in convergence in the left superior frontal gyrus and left superior parietal lobule. The superior frontal gyrus plays a key role in the selection of action sets during switching tasks (Crone et al., 2006; Cutini et al., 2008). Abnormalities in this region could lead to poor performance in maintaining rule-sets (Lao-kaim et al., 2015). This line of studies may suggest that the superior frontal gyrus is important for effectively switching between task-sets and transitioning to new task-set representations. The superior parietal lobule has been attributed to endogenous goal-directed preparation for a switching task (Sohn et al., 2000). This region is the site of visual attentional processing and visuomotor integration (Teixeira et al., 2014), making essential contributions to either maintaining or shifting attention and task rules (Tamber-Rosenau et al., 2011). The involvement of the superior parietal lobule during switching tasks may be due to the attention functioning necessary to successfully switch response sets for achieving task goals. Thus, the superior frontal gyrus and superior parietal lobule may be specifically related to switching.

Working memory. Compared with common EF, working memory showed differences in convergence in the cerebellum. The cerebellum is traditionally associated with timing and temporal sequence of movements (Tavor et al., 2020). Solving working memory tasks may require control of the sequencing of features (Leggio et al., 2008). Thus, the cerebellum may be essential to visual-motor sequencing under time constraints during working memory tasks

(Embury et al., 2019; Yaple & Arsalidou, 2018). Another potential explanation is that activation changes in the cerebellum may reflect differences in response preparation (Salmi et al., 2010). For example, in the 2-back condition during N-back tasks, participants can prepare in advance which button to press, but not in the 0-back condition (Blokland et al., 2011). The 2-back processing demands may induce faster responses so that participants can update their information as fast as possible.

4.2 Development

4.2.1 Common EF

The present meta-analysis has revealed the involvement of the multiple-demand network in common EF in both the adolescent group and the adult group. This is in line with many EF studies focusing on different age samples that have highlighted the engagement of this network underlying general executive demands during EF processes to maintain task goals and activate appropriate behavioral alternatives across adolescence and adulthood (Church et al., 2017; Engelhardt et al., 2019; Yaple & Arsalidou, 2018).

4.2.2 Brain activation specialized for each subcomponent

In adolescents, compared with common EF, both inhibition (part of the multiple-demand network) and working memory (part of the multiple-demand network and bilateral cerebellum) showed differences in convergence, but no difference in convergence was found for switching. As discussed above, the multiple-demand network was activated for general EF processes. Differences in convergence in this network might not be specialized for an EF subcomponent. While for working memory, the individual meta-analysis showed significant convergence in the cerebellum (outside of the multiple-demand network) and the contrast meta-analysis (working memory vs. common EF) revealed differences in convergence in the cerebellum. Combined with previous findings, therefore, we suggest that working memory but not inhibition or switching could be separable from common EF in adolescents.

In adults, compared with common EF, each subcomponent showed differences in convergence. For inhibition, the results pointed toward a special role of the left supramarginal gyrus and left inferior temporal gyrus. Previous studies have linked the supramarginal gyrus with the motor and attentional control required to inhibit a prepotent response (Arrington et al., 2019; Liu et al., 2020). The temporal regions may represent ongoing inhibition processes that underlie task performance (Antons et al., 2019). For switching, our results revealed the involvement of the right superior parietal lobule and left superior frontal gyrus in switching-specific activation. These regions were considered essential for switching between task sets (Tamber-Rosenau et al., 2011). For working memory, our results also highlight the specific involvement of the cerebellum in visual-motor sequencing under time constraints and response preparation. Thus, all three subcomponents could be separable from common EF in adults.

4.2.3 Comparisons between the two age groups for common EF and each subcomponent

Compared with adolescents, adults showed differences in convergence in the prefrontal cortex (inferior frontal gyrus) and superior/inferior parietal lobule for common EF and each subcomponent. Evidence has shown that EF is developmentally correlated with prefrontal activation (Ferguson et al., 2021; Thompson & Steinbeis, 2020). However, the prefrontal cortex matures in the very late period of adolescence and on the transition to adulthood (O’Hare & Sowell, 2008). Lower-level prefrontal activation could lead to poor functioning of selection and control of goal and context information in accordance with EF tasks for adolescents compared with adults (Byrd et al., 2015; Moriguchi et al., 2013). For the parietal regions, maturation of these regions contributes to EF development such that increased activation in these regions is associated with age-related improvements in performing EF tasks (Ciesielski et al., 2006). Furthermore, increasing interregional connectivity between the prefrontal and the parietal regions is associated with developmental changes in EF from adolescence to adulthood (Wendelken et al., 2012). Therefore, we suggest that the sophisticated and flexible function of EF with the involvement of the multiple-demand network, especially for the functional integration between the prefrontal and parietal regions, may not be mature until adulthood.

Besides, for working memory, a difference in convergence was found in the left cerebellum in adolescents compared with adults. This indicates a maturational developmental shift from reliance on the cerebellar regions in young individuals to reliance on the frontal lobe in adults (Ciesielski et al., 2006), suggesting a role of compensatory cerebellar mechanisms in successful performance on working memory tasks.

Overall, our findings may posit that the multiple-demand network places essential neural bases for EF processes. The multiple-demand network has been considered important for diverse cognitive demands (e.g., EF; Duncan et al., 2010). This network may play a central role in the general factor of intelligence (i.e., g), which exhibits strong associations with EF (Cole et al., 2015). Previous studies found that performance on different EF tasks was intercorrelated with g (Barbey et al., 2012), indicating that g may contribute to effective performance on EF tasks (Duan et al., 2010; Engelhardt et al., 2017). Our results identify that common EF mainly recruits the multiple-demand network and reveal different brain regions outside of this network specialized for inhibition (inferior occipital gyrus and temporal regions), switching (superior frontal gyrus and superior parietal lobule), and working memory (cerebellum). Taken together, we suggest a unitary network (the multiple-demand network) underlying both common EF and g. Furthermore, this network may dynamically recruit additional brain regions depending on the demands of a specific subcomponent, explaining distinctions between the processes of a specific EF process and g. Such similarity and differentiation across the multiple-demand network, EF processes, and g should be further explored.

4.3 Task materials

Domain generality. Convergence was commonly found in the bilateral multiple-demand network for each subcomponent in either verbal or nonverbal material. In conjunction analyses, convergence across verbal and nonverbal subcomponents (inhibition, switching, and working memory) was found in the bilateral multiple-demand network. This network is capable of integrating multiple types of information (e.g., perceptual and emotional information) into unified and goal-directed action (D'esposito & Postle, 2015) and thus, we consider this network as domain-general. These findings suggest that highly consistent activation in the multiple-demand network may act on general EF processes, independent of the effects of task materials, indicating that inhibition, switching, and working memory may have a domain-general character.

Domain specificity. Compared with nonverbal domain, verbal inhibition was more associated with the anterior part of Broca’s area (pars triangularis of the left inferior frontal gyrus) and working memory was more associated with the posterior part of Broca’s area (pars opercularis of the left inferior frontal gyrus), whereas no difference in convergence was found for verbal switching. Neuroimaging studies have typically generated interest in Broca’s area, given its essential role in contributing to various language functions (Keller et al., 2009). Specifically, previous studies using fMRI and TMS conclusively showed anatomical specialization in Broca’s area for language functioning (Gough et al., 2005), with the anterior Broca’s area responsible for understanding the meaning of words (semantics; Binder et al., 2009; Ferstl et al., 2008) and the posterior Broca’s area responsible for manipulation and retrieval of word sounds (phonology) and processing syntax (Rodd et al., 2015; Vigneau et al., 2006). Individuals possibly rely on semantic strategies to perform verbal inhibition tasks, whereas rely on both phonemic and syntactic strategies to perform verbal working memory tasks.

Compared with the verbal domain, nonverbal inhibition and nonverbal working memory were more associated with the bilateral precuneus, whereas no difference in convergence was found for nonverbal switching. Brain imaging studies have found consistent activity of the precuneus in various cognitive functions, including visual and spatial processes during EF tasks (Dores et al., 2017; Paulraj et al., 2018). In addition, the precuneus is generally found in eye-movement-related activity (Baumann et al., 2007; Hahn et al., 2006). Given this line of research, our findings suggest that the processing of spatial information through visual input is important in support of performance on inhibition and working memory tasks with nonverbal materials.

In sum, domain-generality across inhibition, switching, and working memory also emphasizes the involvement of the bilateral multiple-demand network for general EF processes, independent of task materials. Regarding domain-specificity, verbal inhibition and verbal working memory are more associated with Broca's area specific to verbal domain, while visuospatial inhibition and visuospatial working memory are more associated with the bilateral precuneus specific to visuospatial domain. Our findings also highlight that working memory may rely on distinct brain regions to coordinate domain-specific information processing and retrieval, in line with the long-term working memory model (Ericsson & Kintsch, 1995).

4.4 Limitations

We could not conduct heterogeneity analyses using I^2 and meta-regressions and we could not statistically examine interactions between different EF comparisons (a specific subcomponent vs. common EF) and age groups with significance testing, because those analyses are not able to be implemented using ALE currently (Müller et al., 2018). Our analyses are within-group contrasts and results can be interpreted as to what extent the three subcomponents could be separable from common EF within adolescents and adults, respectively. We cannot conclude whether the two age groups have significant differences in the differentiation of the EF construct (between-group contrast). Our findings are in general descriptive and need to be further verified with true interaction analyses using advanced neuroimaging tools for meta-analyses.

We initially planned on dividing the age groups into children (<10 years), adolescents (>10 & <18 years), young adults (>18 & <40 years), middle-aged adults (>40 & <65 years), and older adults (>65 years; Andre et al., 2016; Luna et al., 2015). As there were few or no studies on children and older adults, we could not conduct a more fine-grained grouping. The existing brain imaging studies cannot completely address the important question of whether there are differential brain effects on the EF construct across the human lifespan.

To achieve sufficient power for ALE effects, at least 17 experiments in an ALE meta-analysis are needed (Eickhoff et al., 2016), which yields an 80% power to detect an effect size of 0.2, given cluster-level FWE thresholding. In our study, all meta-analyses included more than 17 experiments, except for the meta-analysis of switching in adolescents, which found that switching could not be separable from common EF in adolescents, inconsistent with a previous meta-analysis (McKenna et al., 2017). Such inconsistency may be differences in the age of samples. McKenna et al. included both children and adolescents (6-18 years), whereas we focused on adolescents (10-18 years). Previous studies have identified age-related activation changes in switching between children and adolescents (Durston et al., 2006; Morton et al., 2009) and the two populations should be explored separately. Moreover, McKenna et al. used False Discovery Rate correction, which has been argued not adequate for neuroimaging meta-analyses (Chumbley & Friston, 2009). In contrast, cluster-level FWE correction used in our meta-analyses seems to be the most appropriate method for statistical inference as it entails low susceptibility to false positives (Eickhoff et al., 2016). However, results of switching in adolescents from McKenna et al. and our meta-analyses are both underpowered and should be interpreted with substantial caution due to limited data available by now. Future meta-analyses with sufficient power should clarify the findings of switching in adolescents.

We included the dual-task paradigm into the switching analyses. Miyake et al. (2000) indicated that dual-task performance did not seem to be related to the three subcomponents, but this result should be interpreted with caution. Recently, evidence has converged to the view that the dual-task paradigm involves common cognitive mechanisms as the task-switching paradigm (Hirsch et al., 2018; Koch et al., 2018; Strobach & Schubert, 2017), which is one of the commonly used paradigms to explore the switching process (Kim et al., 2012). It may be reasonable to include dual-task paradigms as switching tasks in our meta-analyses. Nonetheless, we acknowledge that there is still debate on the degree to which the dual-task paradigm taps the underlying switching processes (Fournier-Vicente et al., 2008; Worringer et al., 2019).

Importantly, ALE treats activation foci as spatial probability distributions centered at the given coordinates (Eickhoff et al., 2009, 2012, 2016). The unique information ALE takes into account is the locations (x/y/z coordinates) of the reported activation foci from studies, whereas information about the magnitudes (*t*-values, *p*-values, or *z*-values) of the reported activation foci is not used. In contrast, for effect-size signed differential mapping (ES-SDM), information of the locations and the magnitudes is used (Radua et al., 2012). Thus, ALE determines above-chance convergence of activation probabilities across studies, whereas ES-SDM estimates the combined Hedge’s g across studies. Significant ALE effects are interpreted as spatial convergence of the reported activation foci in those studies (the null-distribution that any spatial association is only happening by chance is rejected; Eickhoff et al., 2009, 2012, 2016; Müller et al., 2018). For example, an ALE individual meta-analysis across studies reporting greater activation in a 2-back compared with the 0-back condition (N-back task) finds convergence in the insula. It shows that greater activation comparing the 2-back with the 0-back condition is more frequently reported in the insula than the rest of the brain across studies, but does not give any information regarding the magnitude of activation in this region.

4.5 Conclusion and implications

Our present meta-analyses show that the multiple-demand network subserves EF processes from adolescence through adulthood. However, this network, especially for the prefrontal and parietal regions, may not be mature until adulthood. In adolescents, only working memory can be separable from common EF, whereas in adults, the three subcomponents can be separable from common EF, indicating a unitary yet partially separable model for adolescents and a unitary and diverse model for adults. For the effects of task materials, inhibition and working memory show both domain-generality and domain-specificity, whereas switching shows only domain-generality.

As discussed, we could not conduct analyses on children and older adults due to restricted data available by now in the field of neurocognitive research on EF. More studies are warranted to examine the neural substrates of the EF construct in those populations. Longitudinal studies may have valuable contributions to a better understanding of EF across development.

The 408 studies in the present meta-analyses recruited tasks commonly used to investigate EF. Activation during EF tasks has been found to be task-dependent (Kim et al., 2012). Take inhibition for example, interference control and behavioral inhibition are two aspects of inhibition (Diamond, 2013). Some tasks may be more associated with interference control (e.g., the Stroop and Flanker tasks), while others may be more associated with behavioral inhibition (e.g., go/no-go and stop-signal tasks). Those tasks have often been conceptualized as taxing the same neural bases of inhibition (Cieslik et al., 2015), as well as neural bases specific to each task (Hung et al., 2018). Such common and distinct neural substrates have also been found for switching and working memory tasks (Kim et al., 2012; Rottschy et al., 2012). Including multiple tasks in meta-analyses to study a specific subcomponent, we may better capture the common functional-anatomical mechanisms underlying this subcomponent and potentially minimize task-specific variance/noises (McKenna et al., 2017). Future meta-analyses may assess brain patterns specific to a task, which in turn supplement our findings.

It is reasonable to assume that activation in performance during an EF task not only reflects the putative EF process but other processes (e.g., perceptual and motor processes). Such a task impurity problem makes the interpretation of results challenging. One common way to solve this problem in behavioral studies is the use of latent variables as dependent measures (Friedman et al., 2008). A latent variable is an underlying ability estimated by extracting the variance shared among multiple tasks and thus, is a pure theoretical measure of the target ability (Friedman et al., 2008). In brain imaging, a similar logic to deal with this problem is to extract the shared activation among multiple tasks to represent the underlying process, indicating the equivalent of latent variable analysis (Collette et al., 2005). Therefore, our findings can be interpreted as capturing the pure EF processes with minimized reduction of task impurity.

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Figure Legend

Figure 1. PRISMA flow chart of the literature search process.

Figure 2. Separate ALE meta-analyses of inhibition (red), switching (yellow), and working memory (green) in the adolescent group and the adult group, respectively (L, left; R, right).

Figure 3. Contrast ALE meta-analyses of each EF subcomponent compared with common EF in the adolescent group (yellow) and the adult group (red), respectively (L, left; R, right).

Figure 4. Contrast ALE meta-analyses of inhibition (red), switching (yellow), and working memory (green) between the adolescent group and the adult group (L, left; R, right).

Figure 5. Contrast ALE meta-analyses of inhibition (red) and working memory (green) between verbal and nonverbal materials (L, left; R, right).