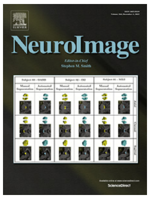
NeuroImage 264 (2022) 119665

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/neuroimage



Inhibition, Shifting and Updating: Inter and intra-domain commonalities and differences from an executive functions activation likelihood estimation meta-analysis

Geraldine Rodríguez-Nieto[a,b,1], Caroline Seer[a,b,1], Justina Sidlauskaite[a,b], Lore Vleugels[a,b,c], Anke Van Roy[a,b], Robert Hardwick[a,b,c,2], Stephan Swinnen[a,b,2,*]

[a] *Movement Control and Neuroplasticity Research Group, Biomedical Sciences, KU Leuven, Tervuursevest 101 box 1501, Leuven 3001, Belgium*
[b] *Leuven Brain Institute (LBI), KU Leuven, Oude Markt 13, Leuven 5005, Belgium*
[c] *Institute of Neuroscience, UC Louvain, Av. Mounier 54, Bruxelles 1200, Belgium*

ARTICLE INFO

Keywords:
Executive functions
Inhibition
Shifting
Updating
Meta-analysis
Cognitive control

ABSTRACT

Executive functions are higher-order mental processes that support goal-directed behavior. Among these processes, Inhibition, Updating, and Shifting have been considered core executive domains. In this meta-analysis, we comprehensively investigate the neural networks of these executive domains and we synthesize for the first time the neural convergences and divergences among the most frequently used executive paradigms within those domains. A systematic search yielded 1055 published neuroimaging studies (including 26,191 participants in total). Our study revealed that a fronto-parietal network was shared by the three main domains. Furthermore, we executed conjunction analyses among the paradigms of the same domain to extract the core distinctive components of the main executive domains. This approach showed that Inhibition and Shifting are characterized by a strongly lateralized neural activation in the right and left hemisphere, respectively. In addition, both networks overlapped with the Updating network but not with each other. Remarkably, our study detected heterogeneity among the paradigms from the same domain. More specifically, analysis of Inhibition tasks revealed differing activations for Response Inhibition compared to Interference Control paradigms, suggesting that Inhibition encompasses relatively heterogeneous sub-functions. Shifting analyses revealed a bilateral overlap of the Wisconsin Card Sorting Task with the Updating network, but this pattern was absent for Rule Switching and Dual Task paradigms. Moreover, our Updating meta-analyses revealed the neural signatures associated with the specific modules of the Working Memory model from Baddeley and Hitch. To our knowledge, this is the most comprehensive meta-analysis of executive functions to date. Its paradigm-driven analyses provide a unique contribution to a better understanding of the neural convergences and divergences among executive processes that are relevant for clinical applications, such as cognitive enhancement and neurorehabilitation interventions.

1. Introduction

Executive functions are a set of higher-level mental processes that are thought to control lower-level mental operations, allowing for successful goal-directed behavior (Diamond, 2013; Friedman and Miyake, 2017). The expression “executive functions” is an umbrella term to describe a variety of related, but dissimilar cognitive functions. This perspective is reflected in the renowned framework of unity and diversity of executive functions (Friedman and Miyake, 2017; Miyake et al., 2000; Miyake and Friedman, 2012). The unity and diversity model distinguishes between Inhibition (i.e., suppressing unwanted or inappropriate actions), Shifting (i.e., mentally switching between different cognitive operations), and Updating (i.e., managing working memory content). While these three facets do not necessarily capture executive functioning in its entirety, they do represent key domains that have been commonly examined across a number of different paradigms (Miyake et al., 2000; Miyake and Friedman, 2012). Typical paradigms to assess Inhibition require the individual to withhold a prepotent or automatic response (Response Inhibition) or to ignore information that is irrelevant for the task at hand (Interference Control) (Friedman and Miyake, 2004). Shifting

---

[*] Corresponding author at: Movement Control and Neuroplasticity Research Group, Biomedical Sciences, KU Leuven, Tervuursevest 101 box 1501, Leuven 3001, Belgium.

E-mail address: stephan.swinnen@kuleuven.be (S. Swinnen).

[1] These authors contributed equally to this work and are joint first authors.

[2] These authors contributed equally to this work and are joint last authors.

https://doi.org/10.1016/j.neuroimage.2022.119665.
Received 22 July 2022; Received in revised form 12 September 2022; Accepted 2 October 2022

is often evaluated using task-switching paradigms, where an individual is asked to switch back and forth between two or more tasks (e.g., categorizing a visual stimulus either according to its color or according to its shape), or dual-tasking paradigms, where an individual performs two tasks simultaneously (Koch et al., 2018). Updating tasks require the individual to store and manage task-relevant information in working memory over a delay for later recall or recognition, and to update this information according to the task context, sometimes after manipulating the information as part of the task (Baddeley, 2012; Baddeley and Hitch, 1994). For instance, an individual may be asked to attend to a number of sequentially presented items and to indicate whether the current item is the same as the item presented a defined number of trials ago (n-back paradigm).

The three “core” executive functions (Inhibition, Shifting, and Updating) have been proposed to give rise to “higher-order” executive functions, such as Planning, whereby an individual needs to rely on multiple executive capacities to successfully simulate and evaluate a sequence of events prior to their execution (Diamond, 2013). Planning is often assessed using a Tower-of-Hanoi paradigm where the individual is asked to re-arrange stacks of plates according to a defined set of rules in as few moves as possible (Sullivan et al., 2009). Moreover, Fluency has been identified as a separable aspect of executive functioning, with relations to more specific executive functioning facets (Gustavson et al., 2019). Fluency is often assessed as verbal fluency, where the examinee is asked to name as many items of a particular category (e.g., animals, vegetables) as possible in a defined time (semantic fluency), or to name as many words as possible that start with a given letter (phonemic fluency).

While executive functions are often associated with the frontal lobe, neuroimaging research has also revealed the involvement of a multiplicity of other brain regions (Stuss, 2011). Specifically, meta-analytic work reported executive functioning tasks to recruit a widespread generalized brain network, including prefrontal and parietal areas (Niendam et al., 2012). While such generalized executive functioning networks seem to be commonly activated across a variety of executive functioning paradigms, more specific subnetworks of consistent brain activation have been identified for dissimilar facets of executive functioning (Niendam et al., 2012; Rae et al., 2014; Rottschy et al., 2012; Worringer et al., 2019; Zhang et al., 2017, 2021).

Meta-analytic endeavors are especially useful in the context of executive functioning research. First, they allow for the evaluation of systematic commonalities between different executive functioning paradigms that supposedly reflect the same underlying capacity. In practice, multiple different variants of similar paradigms are employed to assess the same executive function across studies and research facilities. For instance, dissimilar versions of n-back tasks may be used to assess Updating, and these task versions may differ on several dimensions as a function of the precise research question that they are designed to address (e.g., presentation of verbal vs. non-verbal material, stimulus modality). Aggregating findings over a number of studies based on different task implementations may help abstracting from inferences based on single paradigms. Second, single neuroimaging studies often have to rely on relatively low numbers of participants for economic reasons, which limits their interpretability. Meta-analyses across multiple studies aggregate the information contained in such smaller datasets to enhance statistical power, thereby helping to advance reliable knowledge about human brain functioning. Third, the amount of published literature regarding functional brain activations during executive task performance is continuing to increase, and a comprehensive integration of the current knowledge is warranted. Accordingly, a number of high-quality meta-analyses have been published that shed light on neuroimaging correlates of specific executive functions, namely Inhibition (Nee et al., 2007; Rae et al., 2014; Zhang et al., 2017), Shifting (Wager et al., 2004; Worringer et al., 2019), and Updating (Rottschy et al., 2012; Wager and Smith, 2003). In addition, two meta-analyses have integrated the literature across these facets (Niendam et al., 2012; Zhang et al., 2021). Whereas the first one was published nearly a decade ago, the second one focused on developmental aspects of executive functions from childhood into mid-adulthood, including individuals aged 10–40 years. In summary, previous work from the past ten years has focused on development or has been restricted to a single domain of executive function. Importantly, to the best of our knowledge, there is no meta-analysis that has comprehensively evaluated executive functions networks across the entire span of adulthood while at the same time comparing the neural divergences and convergences among the most frequently used paradigms from the three main domains (Inhibition, Shifting and Updating). The latter point is of considerable relevance, as it is often assumed that paradigms from the same domain are comparable and consistently measure the same psychological process. Therefore, networks previously reported as being distinctive for each domain (Inhibition, Shifting or Updating) carry the bias of being more representative of the paradigm more often included in that particular analysis rather than the full domain (e.g., a meta-analysis being representative of the N-back task but not of the Updating domain). In the current meta-analysis, we aim to alleviate this problem via inclusion of task-specific analyses for the most commonly used paradigms from each of the three main executive domains. Thereby, this enables us to investigate the neural inhomogeneities across them while also extracting the core common neural substrates among them. To the best of our knowledge, this work provides the most extensive and comprehensive synthesis of the executive neural networks to date.

In order to delineate commonalities and differences between brain areas that are activated during the performance of executive functioning paradigms, we rely on the Activation Likelihood Estimation (ALE) algorithm (Eickhoff et al., 2012; Turkeltaub et al., 2012). The ALE approach identifies regions that are consistently activated based on the spatial convergence of peak coordinates from previous studies. These data are compared against a null distribution to identify regions where the clustering of coordinates is statistically above that expected by chance, providing a quantitative synthesis of previous results.

In summary, we aim to identify functional activation that is shared across all commonly used executive functioning paradigms (global analysis). Second, we analyze functional activation that is associated with tasks assessing the three key domains of Inhibition, Shifting, and Updating, respectively (domain-specific analysis). Third, we run fine grained analyses in order to identify typical patterns of neural activation associated with the most frequently used paradigms per domain (paradigm-specific analyses) and we also perform conjunction analyses to identify their commonalities (intra-domain conjunction analyses), revealing the core network of each domain. Fourth, we perform contrast analyses in order to complement the specificity of activation patterns linked to single domains of executive functioning. Finally, we assess which brain regions are recruited across the three key domains (conjunction analysis).

2. Methods

2.1. Literature search

We searched for relevant neuroimaging studies in MEDLINE using PubMed (https://pubmed.ncbi.nlm.nih.gov/) through the following search string: (fMRI OR PET) AND ("attention control" OR "attention regulation" OR "attention shift" OR "attention shifts" OR "attention shifting" OR "attention switch" OR "attention switches" OR "attention switching" OR "attentional control" OR "attentional regulation" OR "attentional shift" OR "attentional shifts" OR "attentional shifting" OR "attentional switch" OR "attentional switches" OR "attentional switching" OR "cognitive control" OR "cognitive flexibility" OR "conflict monitoring" OR "conflict resolution" OR "effortful control" OR "executive attention" OR "executive control" OR "executive function" OR "executive functioning" OR "executive functions" OR "goal directed behavior" OR "goal directed behavior" OR "goal directed control" OR "goal directed response" OR "inhibition" OR "interference resolution" OR "performance monitoring" OR "proactive control" OR "reactive control" OR "self-regulation" OR "set shift" OR "set shifting" OR "set shifts" OR "set switch" OR "set switches" OR "set switching" OR "task shift" OR "task shifting" OR "task shifts" OR "task switch" OR "task switches" OR "task switching" OR "top down control" OR "working memory"). The search yielded 18,370 results published prior to December 31st, 2019. The abstracts of these publications were scanned and pre-selected according to the following criteria: (a) original studies (i.e. review, meta-analysis and case studies were excluded), (b) studies with a sample of healthy individuals of ≥ 18 years old (in case of clinical studies, these were only selected if the results from healthy participants were reported separately), (c) studies using whole-brain analyses, (d) studies that used a standard brain atlas reference (Montreal Neurological Institute or Talairach), (e) results derived from general linear model analyses (e.g., Multivariate pattern analysis, Independent component analysis, probabilistic and connectivity analyses were excluded) and (f) studies targeting executive functions. While our main focus was to examine the three key domains of Inhibition, Shifting, and Updating, we also included paradigms regarding higher level executive functions (e.g., Fluency and Planning) for global analyses across executive functioning domains. Note that the first pre-selection of studies was designed to be very inclusive as to ensure that we would not miss any relevant entries. In a second round, all pre-selected studies were checked again by one of the main authors. Whenever data collectors were not sure about whether a specific study did or did not meet the criteria to be included in further analysis, the record was discussed in more detail among the authors. The selection of the contrasts to be included and the assignment of contrast definitions to specific studies (see below) was deliberated extensively among the authors whenever this was not straightforward to decide.

From the selected studies, results reporting the effect from experimental manipulations (e.g., pharmacological interventions, non-invasive brain stimulation), comparisons with clinical samples, feature comparisons (e.g., age or psychological traits), or contrasts from executive functions paradigms that targeted non-executive components (e.g., saliency, reward, emotion) were excluded, leaving only analyses that targeted the effect of the executive process of interest per se. Likewise, deactivations, correlations, regressions, and connectivity analyses were excluded. Custom code was also implemented to check for and exclude duplicate entries from the same authors (e.g., when data from a previous publication was presented in a newer one for comparative purposes). The final selection of studies comprised a total of 1055 publications, detailing 1633 contrast analyses.

2.2. Data extraction

Data extracted for each experiment included the number of participants and the coordinates of peak activations in stereotaxic (MNI or Talairach) space. Coordinates reported in Talairach space were converted to MNI space using the Lancaster transform (Lancaster et al., 2007). A summary of the data included in each analysis is presented in Table 1.

2.3. Data categorization

The paradigms included in this study were categorized into Inhibition, Updating, Shifting, Fluency and Planning domains. Whereas the Fluency and Planning paradigms were included for the global executive functions analysis, for sub-analyses we only considered Inhibition, Shifting and Updating, for being the most commonly studied domains of executive functioning (Friedman and Miyake, 2017).

Inhibition paradigms required the individual to suppress/inhibit an action or interfering stimuli. Shifting paradigms comprised tasks in which the individual had to switch rules, responses, or tasks. The Updating category included working memory paradigms in which the individual was instructed to either store, manipulate or recall particular information. Within each main domain we identified the most frequently used paradigms for sub-analyses (Table 1). In the case of Updating, we aimed to distinguish between paradigms that require the storage of information in the short-term memory for later recognition (e.g., Sternberg task and Delayed Matching to Sample) and tasks that require participants to store and manipulate the information (e.g., Backward Digit Span). We named the former group 'Recognition' and the latter group 'Manipulation'. Although the N-back task would conceptually be part of the Manipulation group, given the large number of studies (192) using this task, we decided to set it in a separate group (N-back).

Given the large variability in task protocols, even for the same task, great care had to be taken to accurately determine the contrasts for further analysis. Typically, multiple versions exist of any laboratory task, with dissimilar settings depending on specific research questions, idiosyncratic lab protocols, technical considerations, among other factors. For instance, these protocol differences can pertain to stimulus durations, trial numbers, stimulus/response modalities. To ensure that the individual contrasts included in the analyses reflected the cognitive processes of interest (e.g., the No-Go > Go comparison to assess Response Inhibition; see below) rather than other processes also covered by a given protocol (e.g., frequent No-Go > infrequent No-Go or emotional No-Go > neutral No-Go, which would reflect saliency or emotional arousal, respectively, rather than Response Inhibition), we carefully extracted the relevant contrasts for analysis from the original studies and rejected irrelevant comparisons. Where necessary, these decisions were discussed among the authors.

2.4. Data analysis techniques

Activation Likelihood Estimation (ALE) meta-analyses were conducted using custom Matlab scripts. The ALE procedure aims to identify converging clustering of peak activation coordinates (foci) across multiple experiments. Areas in which this convergence is greater than chance are identified by comparison with an empirically determined null distribution. The inherent uncertainty associated with these peak coordinates is addressed by treating each peak as the center of a 3D Gaussian distribution (Eickhoff et al., 2009; Turkeltaub et al., 2002). The revised ALE algorithm reflects the increased spatial reliability of studies with larger sample sizes by modeling them using a narrower Gaussian distribution (Eickhoff et al., 2009). Within-study and within-group effects are minimized by pooling coordinates from suitably similar contrasts within the same publication into a single 'experiment' for analysis purposes (Turkeltaub et al., 2012). In situations where samples with uneven sample sizes were pooled (e.g., studies with groups of younger and older subjects who performed the same task), the smaller of the sample sizes was used to determine the width of the 3D Gaussian distribution used to model the activations for the study in order to provide a more conservative analysis (Eickhoff, personal correspondence, January 14, 2022).

ALE analyses involved a series of steps. First, a modeled activation map was created for each experiment. Modeled activation maps treat each focus from the associated experiment as the center position for a Gaussian distribution (Turkeltaub et al., 2002), the width of which is determined based on the sample size for the experiment (Eickhoff et al., 2009). In a second step, ALE scores were generated to identify the level of convergence across experiments; these ALE scores were calculated by combining the individual modeled activation map for the experiments contributing to the analysis. A third step examined whether the convergence in ALE scores at a given voxel was greater than would be expected by chance. This was achieved by comparing ALE scores to a non-linear histogram integration reflecting the frequency of distinct modeled activation maps (Eickhoff et al., 2012). Results were thresholded at $p < .05$ cluster-level family-wise error (cFWE) corrected for multiple comparisons, cluster-forming threshold at voxel level ($p < .001$) based on empirical simulations indicating that this correction is the most appropriate approach available for statistical inference using ALE (Eickhoff et al., 2016). Results were calculated at 2 mm^3 voxel resolution (volumes were later transformed to 1 mm^3 for reporting purposes). As functional acti-

Table 1

Summary of experiments. Each publication could include multiple contrasts that were eligible for inclusion, but contrasts from the same publication are considered as a single "experiment" in ALE analysis (see methods section for further details). Analyses are only reported for groupings with at least 17 experiments (the minimum required to achieve sufficient power to detect moderate effects when conducting an ALE analysis; Eickhoff et al. 2016).

Analysis	Publications ("Experiments")	Included Contrasts	Subjects in analysis
Global Analysis	1055	1633	26191
Inhibition	416	557	11438
Go/No-Go	136	169	3521
Stroop	106	132	2914
Stop Signal	67	91	1783
Flanker	39	47	1547
Antisaccade	18	25	442
Simon*	18	21	416
Shifting	150	214	3421
Rule / Response Switching	68	80	1841
Wisconsin Card Sorting Test	29	51	528
Dual Task	18	28	352
Updating	492	812	11323
Recognition	205	372	4432
N-back	186	238	4982
Manipulation	82	125	1661

* No converging activation was identified from this task and therefore it is omitted in the next sections.

vations occur predominantly in gray-matter areas, ALE values were calculated only for those voxels with a ≥ 10% probability of containing gray matter (Evans et al., 1994).

Contrast analyses examined areas more strongly associated with one ALE analysis in comparison to another. These analyses were conducted using the resampling procedures outlined in previous random effects ALE subtraction analyses (Eickhoff et al., 2012). First, the observed voxel-wise difference between the two ALE analyses was calculated. Second, experiments contributing to each of the ALE analyses were randomly shuffled into two samples matching the size of the originally observed comparisons. Voxel-wise differences between the ALE score based on these two randomly determined samples were then calculated. Repeating this shuffling procedure 10,000 times generated an empirically determined null distribution against which the observed voxel-wise difference could be compared (note that this label-exchange procedure effectively accounts for comparisons between groups of different sizes). Results were thresholded based on a 95% probability for true differences, and masked based on the respective main effect (Chase et al., 2011; Rottschy et al., 2012). Based on prior work, the minimum volume for reported clusters was 100 mm^3 (Beissner et al., 2013; Erickson et al., 2014; Turkeltaub et al., 2012).

Conjunction analyses were conducted to identify regions that were consistently recruited across different analyses. These conjunctions were calculated by overlaying the respective thresholded activation maps and calculating the minimum statistic for each voxel (Nichols et al., 2005). The minimum cluster volume was set to 100 mm^3 (Beissner et al., 2013; Erickson et al., 2014; Turkeltaub et al., 2012). Specifically, we used conjunction analyses to identify which areas were convergent across the most frequently used paradigms from the same domain (intra-domain conjunctions). Next, with the aim to examine what was specific about one domain (Inhibition, Shifting or Updating) in comparison to the other two, the results of pairwise contrasts (reported in the supplements) were combined using a minimum statistic conjunction approach (domain-specific activations; e.g., (Inhibition > Shifting) ∩ (Inhibition > Updating)). Finally, we also used conjunction analyses to examine the areas that were activated across the three domains (Inhibition, Shifting and Updating). A summary of the conducted analyses is displayed in Table 2.

2.5. Labeling

All results were labeled using their most probable macro-anatomical and cytoarchitectonic/tractographically identified locations according to the SPM Anatomy Toolbox 2 extension (Eickhoff et al., 2005, 2006, 2007). Additional functional labels for motor/premotor regions were provided using the HMAT template (Mayka et al., 2006).

2.6. Data and code availability statement

The individual reports of the studies included in the global analyses and in each category (domains and subdomains), the Matlab codes and resulting NIfTI files can be consulted at: https://osf.io/63pt5/?view_only=f0b3fcad577d4ff39cb4e6f3cd34e63f.

3. Results

3.1. Sample description

A total of 1055 experiments, 1633 contrasts and 26191 healthy participants (≥ 18 years old) were included on this meta-analysis. A detailed summary of the samples included per domain and paradigm is displayed in Table 1.

3.2. Global analysis

In a first analysis, we included all studies that we identified to examine executive functioning, regardless of the domain. Hence, this analysis covered studies from the Inhibition, Shifting, and Updating domains as well as studies assessing Planning or Fluency. In addition, studies relying on paradigms that could not unambiguously be assigned to one of these domains (e.g., hybrid paradigms covering different domains, such as the paradigm described by Wu et al. (2018), who used a numerical version of the Stroop paradigm (Inhibition) with a switching component (Shifting)) were included in this global analysis.

The global analysis (Fig. 1A, Table S1) revealed consistent activation in a fronto-parietal network as well as in the basal ganglia and the cerebellum. The largest cluster of activation spanned the bilateral insular lobes as well as bilateral middle and inferior frontal gyri, with additional peaks in the posterior-medial frontal cortex (pre-supplementary motor area—preSMA) and precentral gyrus. This cluster of activation also spanned the caudate nucleus. A second cluster of activation was found in the bilateral inferior parietal lobules, spanning bilateral superior parietal lobules. This activation extended into the precuneus. Two smaller clusters represented occipito-cerebellar activations in both hemispheres.

Table 2
Summary of analyses.

Name	Description	Analysis
Global Analysis	Executive paradigms from Inhibition, Shifting, Updating, Verbal Fluency and Planning pooled together. Goal: To identify a 'global' (non-specific) network involved in a variety of executive processes	Pooling of data from: Antisaccade, Flanker, Go/No-go, Stop Signal, Stroop, Simon, Dual Task, Rule/Response Switching, Wisconsin Card Sorting, Manipulation, Recognition, N-back, Verbal fluency, Use fluency, Tower of Hanoi, Tower of London and mixed designs
Domain-specific analysis	Inhibition paradigms pooled together.	Pooling of data from: Antisaccade, Flanker, Go/No-go, Stop Signal, Stroop and Simon
	Shifting paradigms pooled together.	Pooling of data from: Dual Task, Rule/Response Switching and Wisconsin Card Sorting
	Updating paradigms pooled together. Goal: To identify the networks specific to each of the three main domains	Pooling of data from: Manipulation, Recognition and N-back
Paradigm-specific analysis	Independent analyses for each of the most frequently used paradigms within Inhibition, Shifting and Updating. Goal: To reveal the neural circuits specific to each paradigm.	Inhibition: Antisaccade, Flanker, Go/No-go, Stop Signal and Stroop. Shifting: Dual Task, Rule/Response Switching and Wisconsin Card Sorting Updating: Manipulation, Recognition and N-back
Intra-domain analysis	Conjunction of the most frequently used paradigms from the same domain. Goal: To reveal the neural convergences among the different paradigms from the same domain (a 'core' domain network).	Inhibition: Antisaccade ∩ Flanker ∩ Go/No-go ∩ Stop Signal ∩ Stroop Shifting: Dual Task ∩ Rule/Response Switching ∩ Wisconsin Card Sorting Updating: Manipulation ∩ Recognition ∩ N-back
Contrast Analysis (Domain-specific analysis)	Conjunction of contrasts analysis Goal: To reveal what is specific to each domain as compared to the others.	Inhibition: Inhibition > Shifting ∩ Inhibition > Updating Shifting: Shifting > Inhibition ∩ Shifting > Updating Updating: Updating > Inhibition ∩ Updating > Shifting
Three domains conjunction – Executive core network	Conjunction of the three domain-specific analyses Goal: to reveal what is common to the three domain-specific networks.	Inhibition ∩ Shifting ∩ Updating

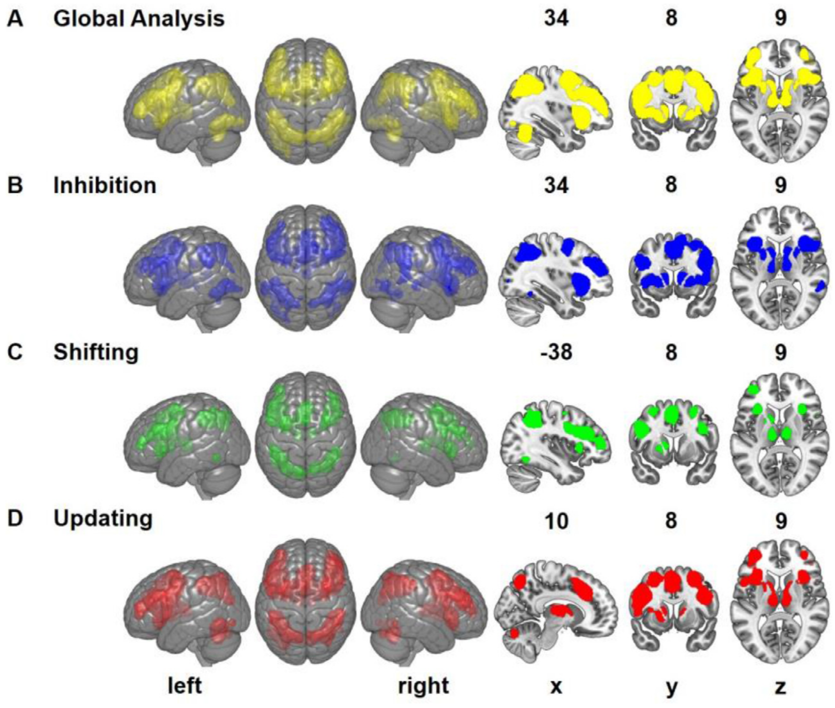


Fig. 1. Brain areas activated by executive functioning tasks across domains (Global Analysis (A)); and by executive functioning tasks taxing Inhibition (B), Shifting (C), and Updating (D). The coordinate from each plane (x-sagittal, y-coronal or z-axial) is indicated above the corresponding slice image.

3.3. *Domain-specific analyses*

3.3.1. *Inhibition*

This analysis covered studies employing paradigms that were exclusively assigned to the Inhibition domain (Table 1). The results (Fig. 1B, Table S2) showed a fronto-parietal network similar to the overall network seen in the global analysis, but slightly more right-lateralized. The largest cluster of activation showed increased recruitment in a right fronto-insular network, with additional peaks in the right basal ganglia (caudate nucleus, putamen) and thalamus. A similar cluster was seen in the left hemisphere. In addition, we identified two parietal clusters (i.e., one in each hemisphere) that both had their maximum peak in the inferior parietal lobule. This activation extended into the superior parietal lobule and precuneus, and it also involved temporal and occipital regions. Two smaller clusters were detected in the left and right occipital cortex. This activation extended into lobule VI of the left cerebellum. In the right hemisphere, peaks were also found in temporal regions.

Paradigm-specific analyses for commonly used inhibition tasks. Independent analyses were run for each of the most frequently used Inhibition paradigms (Fig. 2, Table S3). All paradigms (Antisaccade, Flanker, Go/No-go, Stop Signal, Stroop) recruited activation in medial frontal regions. Activation in the middle frontal gyri was associated with all Inhibition paradigms although to a lesser extent with the Antisaccade. Ac-

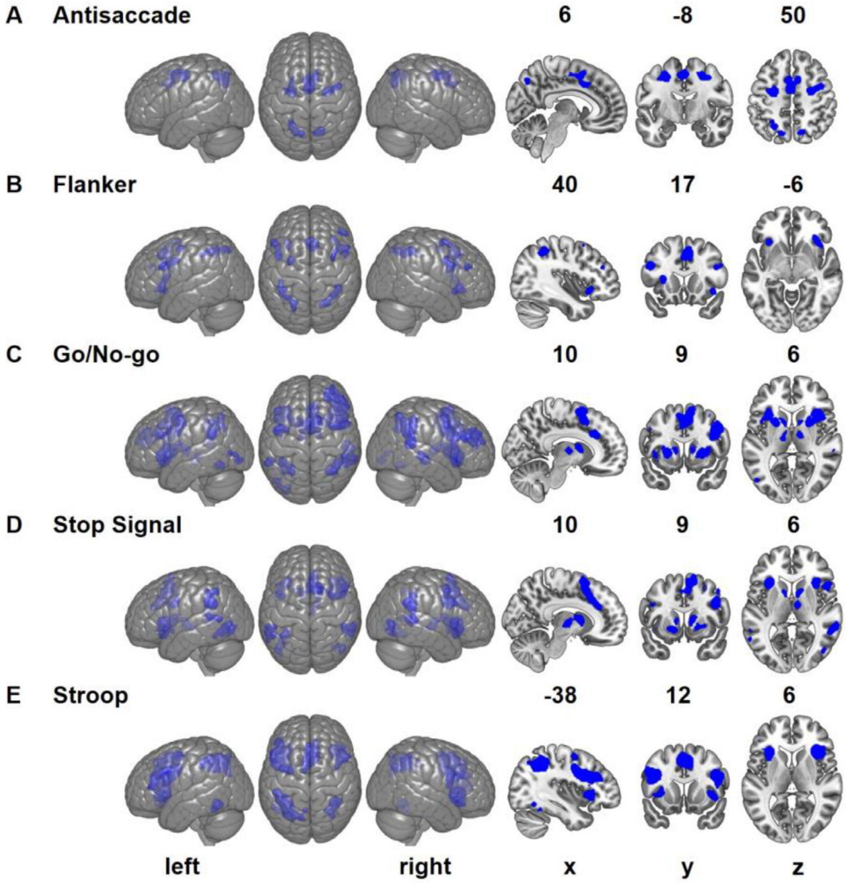


Fig. 2. Brain areas activated by executive functioning tasks from the Inhibition domain. Common paradigms used for examining Inhibition are Antisaccade (A), Flanker (B), Go/No-go (C), Stop Signal (D), and Stroop (E). The coordinate from each plane (x-sagittal, y-coronal or z-axial) is indicated above the corresponding slice image.

tivation in inferior frontal gyri was associated with all paradigms except Antisaccade. Peaks in precentral regions were found for all paradigms. All paradigms except the Antisaccade task also involved prominent insular activations, emerging as fronto-insular-subcortical clusters for the Go/No-go and Stop Signal paradigms. Parietal activations were found for all paradigms, mainly in superior and inferior parietal lobules for all tasks except the Antisaccade. The Antisaccade and Stroop tasks were associated with precuneus activity. Temporal activations were overall rather sparse, but most circumscribed for Go/No-go and Stop Signal tasks. Go-No/go and Stop Signal tasks also consistently recruited subcortical regions. Specifically, Go/No-go paradigms consistently recruited bilateral striatal areas (caudate nucleus, putamen) as well as the bilateral thalami. Similar peaks of activation were found for Stop Signal paradigms, involving basal ganglia nuclei bilaterally (caudate nucleus, pallidum, putamen) and the right thalamus.

Taken together, we observed a pattern of activations that showed similarities across the Inhibition paradigms under investigation, but it also revealed divergent activation patterns that were suggestive of further clustering within the Inhibition domain.

Intra-domain conjunction for inhibition. In order to assess the similarities and differences among the Inhibition paradigms in further detail, we ran conjunction analyses. A conjunction of the five main Inhibition paradigms revealed a single common activation peak in the posterior-medial frontal cortex (preSMA) (Fig. 3A, Table S4).

Next, we conducted conjunction analyses of paradigms with a strong response inhibition component (Go/No-go, Stop Signal; Fig. 3B, Table S5) and of paradigms requiring efficient suppression of interfering information (Flanker, Stroop; Fig. 3C, Table S6). Both conjunction maps overlapped in posterior-medial frontal regions (preSMA), the inferior frontal gyrus (at the inferior frontal junction), and the insula. Activation in the precentral gyrus was found in both types of paradigms. Response inhibition paradigms additionally recruited left occipital and right temporal regions, and they were also associated with significant striatal (caudate nucleus, putamen) and right-lateralized thalamic activations. Interference Control paradigms showed broader activations of the left inferior frontal gyrus.

Contrast analyses: inhibition-specific activation. Contrast analyses were run to detect which brain regions were more consistently associated with Inhibition than with Shifting or Updating. Here we focus on the results obtained from pairwise contrasts with conjunctions (Fig. 4). Additional results obtained from pairwise contrasts are reported in the Supplementary Materials (Table S7).

In comparison to Shifting and Updating tasks, the Inhibition network was associated with more activation in a number of bilateral parietal and right fronto-temporal clusters (Fig. 4A, Table S8). Inhibition-specific activation in right-lateralized fronto-temporal regions were mainly found in the middle and inferior frontal gyri, in the precentral gyrus as well as in medial frontal and cingulate regions and in the right superior temporal gyrus. We also found a cluster of inhibition-specific activation in the left insular lobe. Inhibition-specific parietal clusters were mainly identified in bilateral inferior parietal regions. Finally, we also identified Inhibition-specific activation in right striatal areas, namely the caudate nucleus and putamen.

3.3.2. *Shifting*

This analysis covered studies employing paradigms that were exclusively assigned to the Shifting domain (Table 1). The results (Fig. 1C, Table S9) showed a fronto-parietal network similar to the overall network seen in the global analysis, but with overall smaller cluster size and slightly more left-lateralized (see Fig. 1). The largest cluster of activation was found in the left frontal cortex, spanning the left middle and inferior frontal and precentral gyri. This cluster also included peaks in the left insular lobe and left-lateralized subcortical nuclei, specifically caudate nucleus, putamen, and thalamus. A similar cluster was found in

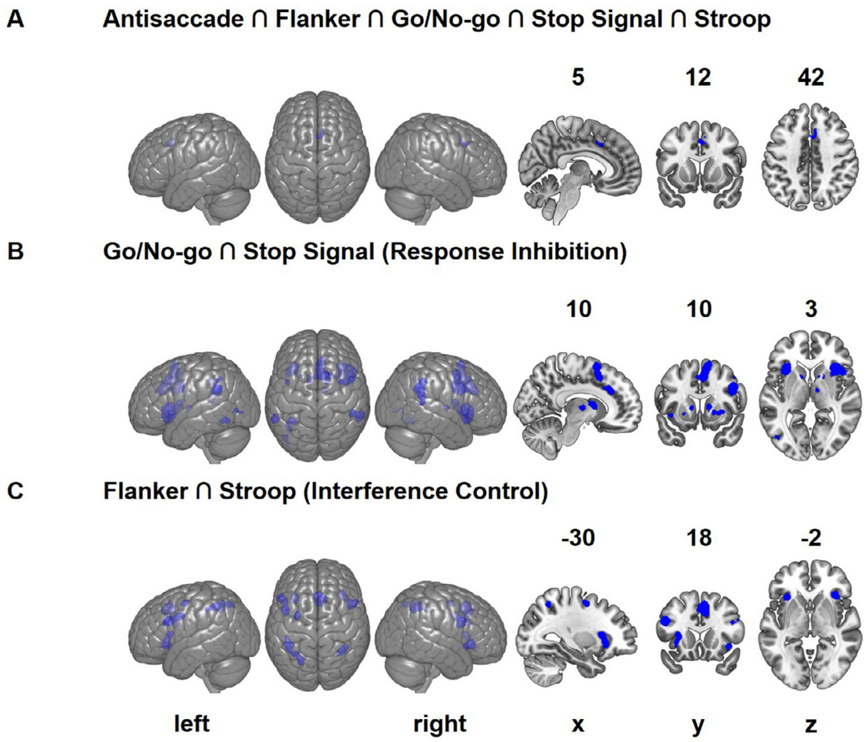


Fig. 3. Intra-domain conjunction analyses within the Inhibition domain. (A) Intra-domain conjunctions across Antisaccade, Flanker, Go/No-go, Stop Signal, and Stroop. (B) Intra-domain conjunctions across Response Inhibition paradigms (Go/No-go, Stop Signal). (C) Intra-domain conjunctions across Interference Control (Flanker, Stroop). The coordinate from each plane (x-sagittal, y-coronal or z-axial) is indicated above the corresponding slice image.

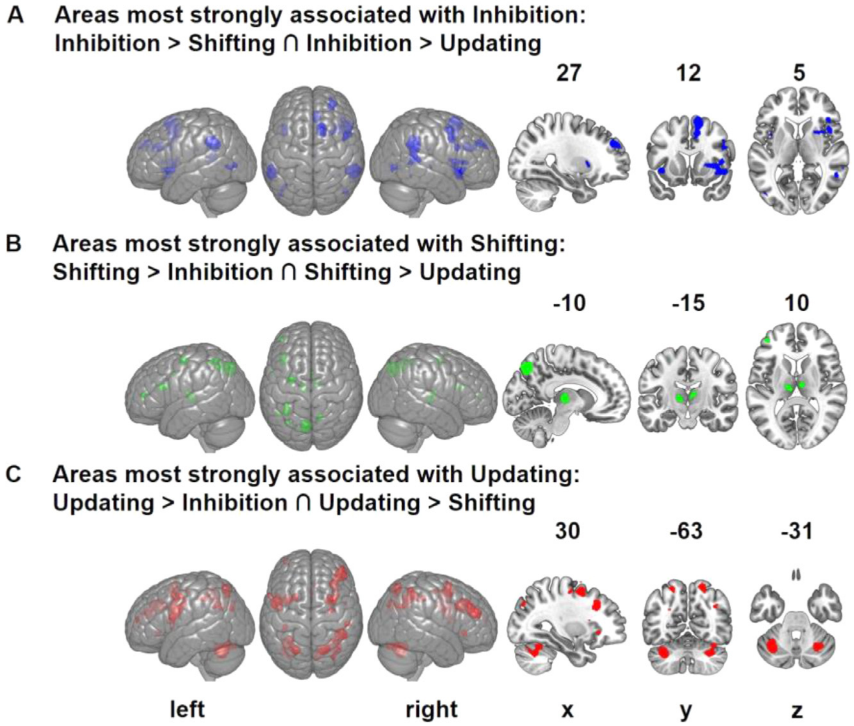


Fig. 4. Brain areas specifically associated with Inhibition (A), Shifting (B), and Updating (C). Slice numbers are indicated above the corresponding slice image. The coordinate from each plane (x-sagittal, y-coronal or z-axial) is indicated above the corresponding slice image.

the right hemisphere, but this cluster was restricted to the right middle and inferior frontal and precentral gyri. Activation was also found in the precentral gyri and in the posterior-medial frontal cortex (preSMA). Bilateral parietal clusters were found, both peaking in inferior parietal regions and extending into the precuneus the superior parietal lobule. A left-lateralized temporo-occipital cluster was also identified, with peaks in the left fusiform and inferior temporal gyri. Finally, a separate subcortical cluster emerged, with a single peak in the right thalamus.

Paradigm-specific analyses for commonly used shifting tasks. Independent analyses were run for the most frequently used Shifting paradigms (Fig. 5, Table S10). For Dual Task paradigms, clusters of activation were exclusively found in the left hemisphere. The activated regions were similar to those found in Rule/Response Switching and in the Wisconsin Card Sorting Test, spanning middle and inferior frontal gyri, the insular lobe as well as superior and inferior parietal regions, on the left hemisphere. In addition, the Rule/Response Switching and Wisconsin Card Sorting paradigms overlapped in the right insula, the right inferoparietal cortex and in the posterior-medial frontal cortex (preSMA). Wisconsin Card Sorting paradigms additionally recruited temporo-occipital regions in the left hemisphere, the right middle frontal gyrus and the thalamus bilaterally.

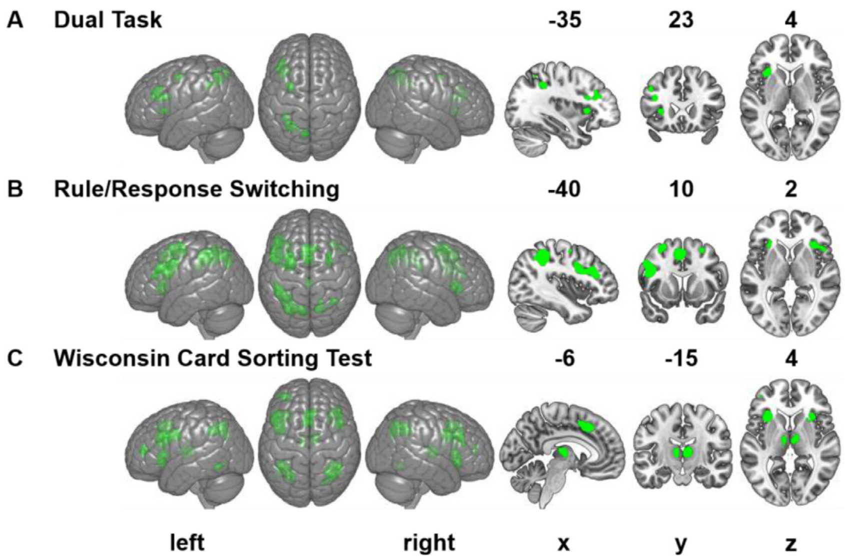


Fig. 5. Brain areas activated by executive functioning tasks from the Shifting domain. Common paradigms used for examining Shifting are Dual Task (A), Rule/Response Switching (B), and Wisconsin Card Sorting Test (C). The coordinate from each plane (x-sagittal, y-coronal or z-axial) is indicated above the corresponding slice image.

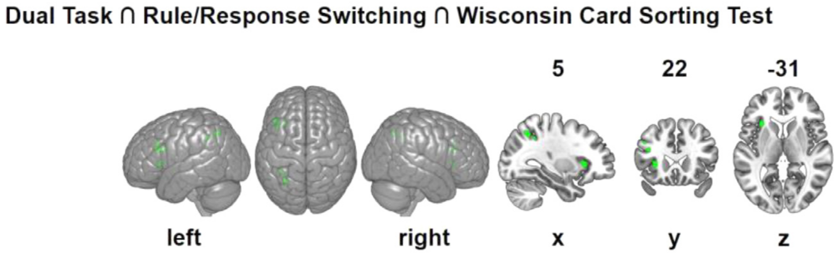


Fig. 6. Intra-domain conjunction analysis within the Shifting domain across Dual Task, Rule/Response Switching, and Wisconsin Card Sorting Test. The coordinate from each plane (x-sagittal, y-coronal or z-axial) is indicated above the corresponding slice image.

Intra-domain conjunction for shifting. The intra-domain conjunction analysis (Fig. 6, Table S11) revealed common clusters of activation for the Dual Task, Rule/Response Switching and Wisconsin Card Sorting in the left insular lobe, the left middle and inferior frontal gyri as well as in the left superior and inferior parietal lobules.

Contrast analyses: shifting-specific activation. Contrast analyses were run to detect which brain regions were more consistently associated with Shifting than with Inhibition or Updating (Fig. 4). Results obtained from pairwise contrasts are reported in the Supplementary Materials (Table S12).

In comparison to Inhibition and to Updating tasks, Shifting tasks were associated with more activation mainly in the left hemisphere (Fig. 4B, Table S13). This left-lateralized Shifting-specific activation spanned frontal (mainly middle and inferior frontal gyri, but also the left posterior-medial cortex—preSMA—and precentral gyrus) and parietal (superior and inferior parietal lobule, precuneus) areas. In the right hemisphere, Shifting-specific activity was mainly detected in the parietal lobe (superior parietal lobe, precuneus). In addition, Shifting was specifically related to areas of the bilateral thalami.

3.3.3. Updating

This analysis covered studies employing paradigms that were exclusively assigned to the Updating domain (Table 1). The results (Fig. 1D, Table S14) showed a fronto-parietal network similar to the overall network seen in the global analysis. The largest cluster was detected in the left hemisphere, spanning frontal (middle and inferior frontal gyri, precentral gyrus, posterior-medial frontal cortex/preSMA), insular and subcortical (thalamus, striatum) regions. A similar cluster was detected in the right hemisphere. Parietal clusters were present in both hemispheres, spanning the superior and inferior parietal lobules and precuneus. Furthermore, three cerebellar clusters were found for Updating. The first cerebellar cluster peaked in the left crus I and extended into the left inferior occipital gyrus. A second cerebellar cluster peaked in the right lobule VI and extended into the right inferior temporal gyrus. Finally, a separate cluster was identified spanning the bilateral crus I of the cerebellum.

Paradigm-specific analyses for commonly used updating tasks. Independent analyses were run for Manipulation, Recognition and N-back paradigms (Fig. 7, Table S15). All paradigms were associated with bilateral activation in the middle frontal gyrus, the inferior parietal lobe, the posterior-medial frontal (pre-SMA) and insular cortices. The N-back was associated with a prominent bilateral activation in the caudate and in the thalamus and Recognition paradigms were associated with activation in the thalamus, the caudate and the putamen on the left side. Interestingly, all Updating paradigms consistently recruited right cerebellar regions (crus I, lobule VI) and only the N-back and Manipulation paradigms recruited this region on the left side.

Intra-domain conjunction for updating. The conjunction analysis within the Updating domain (Fig. 8, Table S16) revealed that Manipulation, N-back, and Recognition paradigms showed common activation patterns in superior, middle and inferior frontal gyri, medial frontal areas, insular lobes, and parietal regions (superior and inferior parietal lobes, precuneus). We also detected consistent common recruitment of lobule VI of the right cerebellum.

Contrast analyses: updating-specific activation. Contrast analyses were run to detect which brain regions were more consistently associated with Updating than with Inhibition or Shifting (Fig. 4). Results obtained from pairwise contrasts are reported in the Supplementary Materials (Table S17).

In comparison to Inhibition and to Shifting tasks, Updating tasks consistently recruited more activation in a number of fronto-parietal and cerebellar areas (Fig. 4C, Table S18). Updating-specific activity in the frontal lobes was centered on the middle frontal gyri as well as precentral and postcentral gyri. Parietal activations spanned bilateral superior

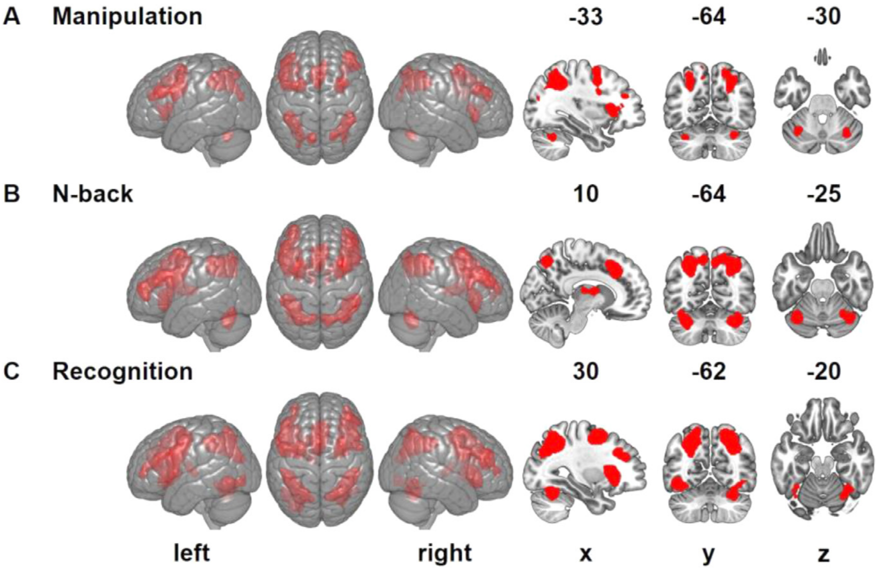


Fig. 7. Brain areas activated by executive functioning tasks from the Updating domain. Common paradigms used for examining Updating are Manipulation (A), N-back (B), and Recognition (C). The coordinate from each plane (x-sagittal, y-coronal or z-axial) is indicated above the corresponding slice image.

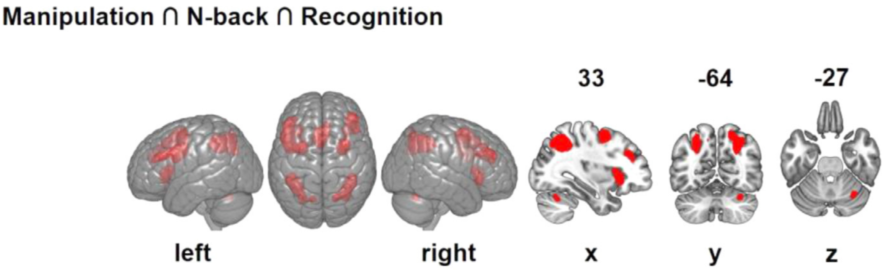


Fig. 8. Intra-domain conjunction analysis within the Updating domain across Manipulation, N-back, and Recognition. The coordinate from each plane (x-sagittal, y-coronal or z-axial) is indicated above the corresponding slice image.

and inferior parietal lobules. Interestingly, Updating was prominently and specifically associated with cerebellar activations (mainly left crus I and right lobule VI).

3.4. *Conjunction analyses to reveal the core executive network*

Conjunction analyses were run to detect brain areas that were consistently recruited across the three key domains of executive functioning (Inhibition ∩ Shifting ∩ Updating) (Fig. 9, Table S19).

Common brain activation recruited by Inhibition, Shifting, and Updating tasks was consistently found in a large fronto-parietal network similar to the one identified in the global analysis (Fig. 9). This network can be considered a ‘core’ executive functioning network, as activation associated with these clusters overlap across the three main executive functioning domains under investigation. This network comprised activations in bilateral frontal cortices, centered on the middle and inferior frontal gyri. Activation peaks were also found in the insular lobe and in the posterior-medial frontal cortex (preSMA). Parietal activations spanned superior and inferior parietal lobules and precunei. Consistent activation was further observed in a left-lateralized temporo-occipital cluster (fusiform and inferior temporal gyri). There was also consistent subcortical activation, in bilateral thalami as well as left caudate nucleus and pallidum.

In concordance with the principles of Data Sharing and Transparency, the 3D maps of the above mentioned results (NIfTI files for global, domain and task analyses) are available at https://osf.io/d85pb/?view_only=f0b3fcad577d4ff39cb4e6f3cd34e63f.

4. Discussion

In this meta-analysis we comprehensively integrated the existing neuroimaging findings on executive functions in adults, modeling the available data of 1055 experiments including 26,191 participants. We aimed to identify the ‘global’ network for executive functions as well as the common and distinct networks from the main executive function domains (Inhibition, Updating, and Shifting). Importantly, we provided for the first time a comprehensive and extensive meta-analysis of the most commonly used executive function paradigms and we reported about the convergences and divergences among them. We observed that executive functions recruit a fronto-parietal network, as well as temporo-parietal association areas, thalamus and basal ganglia, consistent with previous literature. Whereas Inhibition, Updating and Shifting showed overlaps within these regions, each of these domains also showed distinct patterns of activation. Our paradigm-specific and intra-domain conjunction analyses (conjunction of the paradigms from the same executive domains) allowed a fine-grained comparison among paradigms from the same executive domain and a more refined study of the distinctive networks from each executive domain. Among the most remarkable findings that this approach revealed are: (a) important heterogeneities among the paradigms targeting Inhibition, (b) a conspicuous laterality of Inhibitory and Shifting domains, and (c) the identification of neural signatures associated to the specific modules of the Working Memory model from Baddeley and Hitch (1974, 1994).

4.1. *The ‘global’ and ‘core’ executive network*

The ‘global’ Executive Functioning network revealed a widespread activation across bilateral fronto-parietal regions, insula, basal ganglia, and occipital regions, extending to the cerebellum. The ‘core’ executive network, derived from the conjunction among Inhibition, Updating and Shifting, showed a substantial overlap across cortical and subcortical regions. However, the core executive functioning network involved a less extensive activation in the bilateral middle frontal gyrus, and did not engage the cerebellum. Whereas the global map is more comprehensive

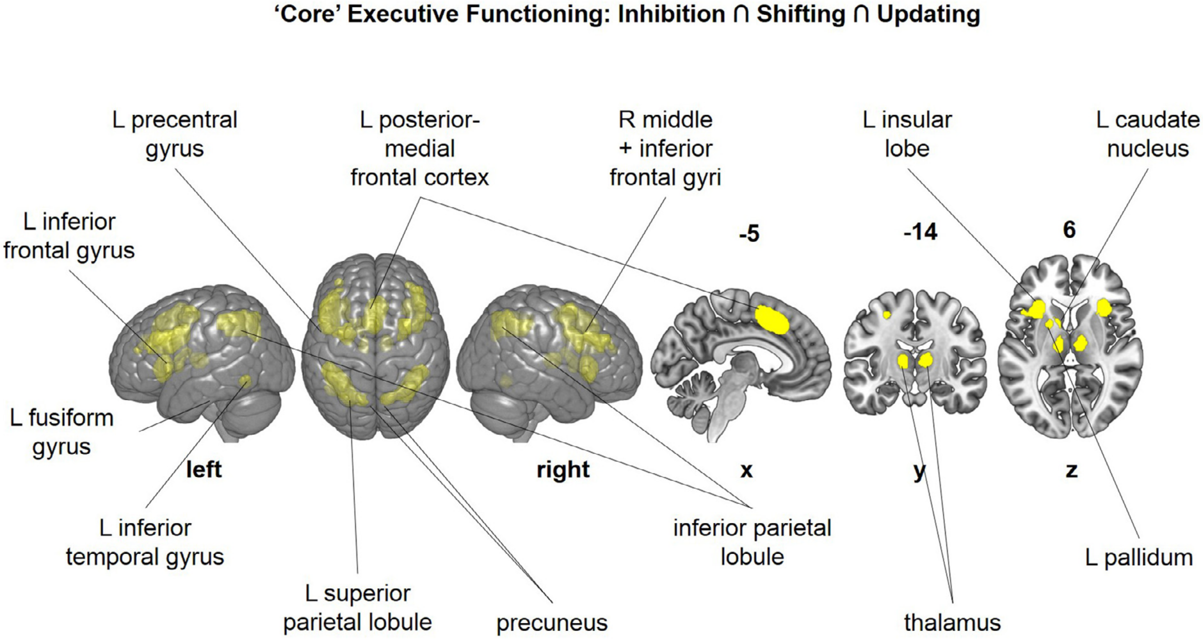


Fig. 9. Brain areas commonly recruited by Inhibition, Shifting, and Updating (Inhibition ∩ Shifting ∩ Updating), representing a 'core' executive network. The coordinate from each plane (x-sagittal, y-coronal or z-axial) is indicated above the corresponding slice image. L = left, R = right.

regarding the type of executive processes included (fluency, planning, and mixed paradigms, in addition to the three main domains), the conjunction map shows what is common to the three main domains. Hence, the 'global' network is comprehensive regarding the most frequently active regions in a variety of executive function processes, whereas the 'core' network shows more uniquely what is consistent across the three main domains.

The convergence of the neural substrates from the three main domains into a 'core' network is well in line with the conceptual notion of a latent common Executive Functioning factor at a behavioral level (see Friedman and Miyake 2017, Miyake and Friedman 2012, Seer et al. 2021). In this sense, the core network reflects the coalescence in common cognitive processing requirements among the three main domains, and therefore, supports the concept of executive function as a common general domain (Miyake and Friedman, 2012). This common cognitive processing may imply sustained attention, monitoring and coordination of simultaneous cognitive processes, necessary to accomplish a particular task. Some classic perspectives consider the maintenance and management of goals in spite of interference, top-down bias and competition resolution at the core of executive processing (Friedman and Miyake, 2004; Kane and Engle, 2002; Miller and Cohen, 2001). In this respect, the concept of 'executive' function implies the orchestration of different cognitive sub-processes in order to achieve a goal (Cristofori et al., 2019). Therefore, the term represents processes that enable us to organize and plan our thoughts and behavior, which is crucial in novel situations and/or problem-solving contexts (Diamond, 2013) and can be considered essential for functional independence in everyday life across the lifespan.

The 'core' executive network observed here has long been shown to be engaged in a variety of tasks that include an executive component (Fedorenko et al., 2013; Lemire-Rodger et al., 2019; Niendam et al., 2012). Among the regions shown in the 'global' and 'core' executive networks we observed the inferior frontal junction, the inferior parietal lobe, the insula and the preSMA. The inferior frontal junction (junction of the inferior frontal sulcus and the inferior precentral sulcus) has been proposed to represent abstract task-relevant properties of objects (Brass et al., 2005). Being located in the vicinity of language, memory and cognitive control related regions, it has been proposed to serve as a bottleneck between top-down and bottom-up processing. The inferior frontal junction is functionally distinguished by its connectivity with the inferior parietal lobe, the anterior insula, and the preSMA, which were all observed in the 'core' network (Muhle-Karbe et al., 2016). The fronto-parietal network that we observed presents a large overlap with networks identified for broader cognitive domains such as attention, a 'multiple-demands' system (organized to perform higher cognitive operations), reasoning and fluid intelligence (Ardila et al., 2018; Camilleri et al., 2018; Duncan, 2010; Langner and Eickhoff, 2013; Müller et al., 2015). These different processes are interrelated (conceptually and empirically) and involve similar cognitive requirements such as goal maintenance and attention control. Friedman and Miyake (2017) discuss in detail the relation between executive functions, the multiple-demand system, attention and fluid intelligence at a conceptual and behavioral level. Future neuroimaging meta-analyses may compare the neural networks underlying these different constructs.

In addition to prefrontal and parietal areas, we observed that the 'global' and 'core' executive function networks engaged the striatum extending to the thalamus. This might suggest a circuit involving prefrontal, thalamic and striatal projections, which has shown to be crucial in the synchronization and planning of cognitive-motor outputs (Florio et al., 2018). Interestingly, a multi-scale connectomics approach, based on structural and functional connectivity maps, has revealed a major role of the fronto-striato-thalamic circuit in brain aging (Bonifazi et al., 2018). Deterioration in this circuit may contribute to executive function deficits in older adults.

The 'global' and 'core' executive maps also displayed activation in the fusiform gyrus, which has been recognized as a pattern recognition processing area (Weiner and Zilles, 2016). However, the more fine-grained intra-domain conjunction maps did not show activations in the fusiform gyrus, the thalamus or the striatum, indicating that these regions are activated only in particular paradigms within each domain. Recent evidence shows the existence of sub-networks in the executive system (Camilleri et al., 2018). One of these sub-networks is composed by the thalamus and the putamen. As we will discuss in the next sections, this loop seems to be relevant only in particular executive processes.

4.2. Inhibition network

The Inhibition network involved areas associated with monitoring and error detection (anterior and mid-cingulate cortex), motor control (precentral gyrus and basal ganglia), attentional control (inferior frontal gyrus) and multisensorial integration (supramarginal and angular gyri). According to the contrast analyses, these areas were also recruited to a higher extent in Inhibition as compared to Shifting and Updating, further underscoring their key role in Inhibition. Referring to the ability to suppress a response or stimulus, Inhibition requires constant monitoring, and the participant is usually aware of mistakes whenever these occur; this pattern is not always reflected during Shifting and Updating.

Nonetheless, it has been debated whether the fronto-parietal network recruited during inhibition constitutes a salience detection network vs a distinctive inhibitory network (Criaud and Boulinguez, 2013; Swick et al., 2011; Wijeakumar et al., 2015), as well as which modules are really crucial for processing inhibition (Sebastian et al., 2016). For many years, the right inferior frontal gyrus was considered as a potential central node in the inhibitory process (Aron et al., 2014). However, subsequent studies have shown that this node and others in the network (precentral gyrus, inferior parietal lobe and striatum) are engaged in the processing of salient non-inhibitory stimuli and sustained attention (Erika-Florence et al., 2014; Langner and Eickhoff, 2013; Sebastian et al., 2021; Wijeakumar et al., 2015). To that extent, inhibitory processes imply salience detection per se, and inhibition is mostly challenged when the individual is faced with salient interfering stimuli. A recent approach argues that the perception of different types of unexpected events invariably leads to action slowing or stopping and that this phenomenon explains the common recruitment of a fronto-basal ganglia network (right inferior frontal gyrus, preSMA and subthalamic nucleus) in unexpected events perception and action stopping (Wessel and Aron, 2017).

Although the middle and superior frontal gyri have been less discussed in the literature on inhibitory processes, a systematic study of patients with brain damage revealed that the performance on two inhibitory tasks (Stroop and Hayling) relied on the integrity of these structures (Cipolotti et al., 2016). The results from our present meta-analysis also show that the middle frontal gyrus is consistently recruited during inhibitory paradigms. Whether this reflects a critical role of the middle frontal gyrus, or whether inhibition is the result of dynamic properties among the components of a network remains to be further investigated.

To our knowledge this is the first meta-analysis that directly compares the neural networks of the five most commonly used inhibitory paradigms: Go/No-go, Stop Signal, Stroop, Flanker and Antisaccade. Notably, the intra-domain conjunction and paradigm-specific maps revealed that not all these classic inhibition tasks share the same robust network. When all paradigms were considered, only the preSMA region emerged as a common region. Further analyses led us to regroup the paradigms according to cognitive similarities: Response Inhibition (Go/No-go and Stop Signal) and Interference Control (Stroop and Flanker). Whereas the former group implies stopping or canceling an action, the latter is more focused on overriding conflicting information. We found that both maps showed activation in the preSMA, the insula, the inferior frontal junction and different but adjacent portions of the inferior parietal lobe. These regions are part of the common unexpected action and inhibition network found by Sebastian et al. (2021). However, as noticed in the previous section, they are not specific to the Inhibition domain. Furthermore, they do not match for the most part with the unexpected events network (right inferior frontal cortex, subthalamic nucleus and preSMA) proposed by Wessel and Aaron (2017).

Remarkably, the Response inhibition map showed, in addition, activation of the thalamus, the basal ganglia and regions belonging to the ventral attention network (inferior frontal and supramarginal gyri) which is thought to act as detector of salient stimuli, in contrast with the top-down dorsal attention network (Corbetta and Shulman, 2002). Moreover, the right inferior frontal cortex is part of the unexpected events - inhibition network (Sebastian et al., 2021; Wessel and Aron, 2017). Response inhibition tasks are characterized by the presentation of infrequent and therefore de facto salient stimuli. Although Interference Control also involves the detection of unexpected (incongruent) events, the crucial difference with Response Inhibition might be a bottom-up detection of salient information.

In contrast with the proposition of Wessel and Aron (2017) and with the observations of Sebastian et al. (2021), we did not find activation in the subthalamic nucleus for Response inhibition. When looking at the individual Inhibition task maps, only one cluster from the Stop Signal paradigm (action cancellation) was bordering this region. It has been proposed that the subthalamic nucleus reflects an emergency-like system (Hannah and Aron, 2021), thus, it is possible that some fMRI protocols lack temporal resolution to detect the fast changes in this region and/or that this region may be more crucial in circumstances when the need for stopping is rather unforeseen.

Interference Control paradigms showed an activation in the left middle frontal gyrus (bordering the inferior frontal sulcus), not present in the Response inhibition map. This cluster was adjacent to one identified in Shifting paradigms and might reflect a possible functional gradient relevant in inhibiting distracting information and alternating between different cognitive processes (flexibility). Overall, these findings reinforce the idea that inhibition is a generic term that encompasses rather heterogeneous behaviors as supported by behavioral and clinical observations (Bissett et al., 2021; Friedman and Miyake, 2004; Hedden and Yoon, 2006; Nigg, 2000; Seer et al., 2021). At least, the present neural evidence supports its distinction in Response Inhibition and Interference Control which may further inform conceptual delineation.

Response inhibition paradigms engaged the basal ganglia and the thalamus, in concordance with previous observations (Coxon et al., 2016; Guo et al., 2018; Hung et al., 2018; Swick et al., 2011; Zhang et al., 2017). Interestingly, we did not observe this for Interference Control paradigms. Although some meta-analyses reported basal ganglia activation in cognitive inhibition paradigms (Stroop and Think/No-think), this pattern has been inconsistent (Huang et al., 2020; Hung et al., 2018; Swick et al., 2011; Zhang et al., 2017). Although the more consistent activation of basal ganglia for Response inhibition paradigms seems to point to a central role in motor control (performing or withholding movement), these structures were also activated in some Updating paradigms, as will be further discussed.

Making a further distinction within Response inhibition tasks, we observed that the Stop Signal, but not the Go/No-go task recruited the red nucleus, which is involved in motor coordination. The distinctions regarding the basal ganglia and midbrain activations could have potential implications for the diagnostics and treatment of motor control disorders.

The insula was shown to be engaged by the Go/No-go, Stop Signal, Stroop and Flanker paradigms. Previous studies have shown insular activation to relate to task performance in inhibition paradigms (Cai et al., 2014; Coxon et al., 2016; Wager et al., 2005). Nonetheless, the insula is also part of the vigilant attention network (Langner and Eickhoff, 2013), making it more challenging to disentangle its particular function in the inhibitory process.

In sum, our paradigm-specific approach underscores the complexity of Inhibition as a single construct. Moreover, several qualifications emerge from this analysis: (a) the inferior frontal gyrus is not a consistent node across Inhibition paradigms and is rather relevant when saliency detection is involved, (b) the Response inhibition paradigms are distinctively characterized by the activation of the ventral attention network, basal ganglia and thalamus, (c) the inferior frontal junction and the insula are common nodes among Response inhibition and Interference Control paradigms, yet these regions are also recruited by the other executive domains, as discussed in the previous section, and (d) the Antisaccade paradigm seems to have minimal neural commonalities with other Inhibition paradigms, suggesting that antisaccade-type inhibition might differ from inhibitory processes reflected in Response Inhibition and Interference Control tasks in that it recruits different brain areas. As such, its individual use as an Inhibition index in clinical and experimental settings should be carefully considered. While more detailed analyses regarding differences among antisaccade paradigms were beyond the scope of the present work, we would like to refer interested readers to the database that we publish together with this paper for follow-up analyses regarding heterogeneity among antisaccade tasks in the existing literature.

4.3. *Shifting network*

Among the areas that were more active during Shifting as compared to Inhibition and Updating, the most prominent were the left inferior and superior parietal lobes, the precuneus, the thalamus, and the left inferior and middle frontal gyri. Whereas the inferior parietal lobe is consistently active across different executive domains the activation of the precuneus and superior parietal lobe is consistent for Shifting, but not for Inhibition and Updating (Niendam et al., 2012; Worringer et al., 2019; Zhang et al., 2017, 2021). Notably, Zhang et al. (2021) also found a greater activation in these regions in Shifting as compared to Inhibition and Working Memory, which highlights the core role of these regions in Shifting processes.

Diffusion weighted imaging studies have identified the precuneus as being part of a central structural core (Hagmann et al., 2008). It is also a heterogeneous brain region from an anatomical and structural connectivity viewpoint with three subdivisions that have a distinct connectivity profile (anterior, central and posterior). Furthermore, a recent study suggested that it mediates the interaction among the dorsal attention, the default mode and fronto-parietal control resting state networks (Luo et al., 2020), which supports its role in switching between different cognitive processes.

To our knowledge this is the first meta-analysis that compared and integrated the neural networks of the three most common Switching paradigms: the WCST, Dual Task and Rule/Response Switching. This revealed notable differences, but also commonalities, among the neural nodes associated with these paradigms. First, the paradigm-specific analyses revealed that the precuneus was identified as a node of Dual Task and Rule/Response Switching, but not of the Wisconsin Card Sorting Test paradigm, in which individuals are required to switch classification criteria but the rules and task context remain constant, unlike in the other two Shifting subdomains. Thus, by virtue of its central location and heterogeneous connectivity profile, the precuneus may play a central role in the interaction between different networks and may be crucial in the ability to switch between different cognitive frames (e.g., different rules or tasks). Second, the anterior portion of the left middle frontal gyrus and the thalamus were active during the Wisconsin Card Sorting Test but not the Dual Task or Rule/Response Switching. These regions were also active in the Updating general map (and in the N-back and Recognition tasks) which may point to the higher working memory load during the Wisconsin Card Sorting Test as compared to the two other Shifting subdomains. Third, the Rule/Response Switching and the Wisconsin Card Sorting Test (but not the Dual Task) recruited the preSMA region -similar to Inhibition tasks-, which has not only been related with action stopping but also, more generally, with action selection (Rae et al., 2014). In addition, whereas the Dual Task exhibited activation exclusively in the left hemisphere, the Wisconsin Card Sorting Test and the Rule/Response Switching paradigms also exhibited fronto-parietal activation in the right hemisphere (although to a lesser extent than in the left side). This finding may point to a crucial role of preSMA and bilateral fronto-parietal activation in sequential as compared to parallel Shifting processing.

According to the intra-domain conjunction analysis for Shifting, the three main Shifting tasks commonly activated the inferior and superior parietal lobes, the inferior frontal gyrus pars triangularis, the middle frontal gyrus and the insula, all in the left hemisphere. Although Inhibition and Shifting engaged fronto-parietal regions bilaterally (according to the general maps), Inhibition recruited to a greater extent portions of the right hemisphere than the two other executive domains, while Shifting engaged left regions to a higher extent (according to the contrast maps and the intra-domain conjunction analysis). A transcranial magnetic stimulation study found that the middle frontal gyrus plays an important role in the reorganization and regulation of brain networks. Whereas the right middle frontal gyrus is associated with sustained attention, the left middle frontal gyrus is associated with selective attention (Song et al., 2019). To this regard, the Shifting processing tasks seem to demand more selective attention as compared with Inhibition tasks.

In sum, whereas the Shifting network recruits bilateral fronto-parietal areas, the regions that are more strongly associated to Shifting as compared to the other two domains and that are also consistent across the subdomains (Dual Task, Rule/Response Switching and Wisconsin Card Sorting Test) are noticeably lateralized to the left hemisphere. Moreover, whereas the WCST seems to have a higher overlap with the Updating network as compared to the two other Shifting paradigms, the preSMA seems an important node in distinguishing sequential (WCST and Rule/Response Switching) from parallel Shifting (Dual Task). Finally, the precuneus and the left middle frontal gyrus seem to be of particular relevance for the interaction and reorganization of neural networks, which might be at the core of Shifting and flexible processing in general.

4.4. *Updating network*

The regions engaged to a higher extent in Updating as compared to Shifting and Inhibition were the right middle frontal gyrus (central portion), the left inferior frontal junction (junction of the inferior frontal sulcus and the inferior precentral sulcus), the superior parietal lobe bilaterally, and the left cerebellum. All these regions were consistently engaged by the three main Updating tasks. In addition, as apparent from the intra-domain conjunction analyses, the Updating domain was the one that showed a more distributed and robust network common to the subdomains (Recognition, Manipulation and N-back). Furthermore, the pattern from the Updating intra-domain conjunction map covered most of the intra-domain conjunction maps of Inhibition and Shifting, whereas the latter two showed a negligible overlap. This suggests that the central cognitive components of Updating are common to those of Inhibition and Shifting, whereas the central cognitive components between Inhibition and Shifting seem more independent.

Besides the Updating tasks, the right middle frontal gyrus also showed up in the Go/No-go and Flanker (and to a minor extent the Wisconsin Card Sorting Test) activation maps. Similar to the right inferior frontal gyrus, the right middle frontal gyrus has been associated with sustained and vigilant attention (Langner and Eickhoff, 2013; Song et al., 2019). Sustained attention seems crucial in Updating paradigms and individuals must be vigilant of information sets and avoid distractions in order to maximize their performance.

Besides being active in the three Updating paradigm types (and engaged to a higher extent in the Updating domain), the left inferior frontal junction was also active in the Stroop, Wisconsin Card Sorting Test and Rule/Response Switching paradigms. This observation is consistent with previous findings supporting the role of this region in the updating of mental representations in different executive domains (Derrfuss et al., 2005). As mentioned before, this region has been proposed to represent abstract information of objects, possibly by integrating information from language, working memory and motor control (Brass et al., 2005).

Although a small portion of the superior parietal lobe was engaged to a greater extent in Updating than in Shifting and Inhibition domains, this region was not only engaged in all Updating tasks but also in most of the Inhibition and Shifting tasks (only the Wisconsin Card Sorting Test and Stop Signal were the exception). This region is involved in a wide range of cognitive functions such as attention, visual perception, spatial cognition and reasoning (Wang et al., 2015). Accordingly, although it generally appears to contribute to the executive domain, its role is not exclusive and covers a broad range of functions.

The most distinctive activation from the Updating domain was located in the cerebellum. Recruitment of the cerebellum was present not only in the domain-level analysis of Updating, but also for each of the Updating paradigm-specific analyses (i.e. N-back, Recognition, and Manipulation). Consistent recruitment of the cerebellum at both the domain and task-level was unique to Updating. This is noteworthy as there has been a long history of research arguing that the cerebellum is not only critical to motor control, but also plays an important role in working memory (Beuriat et al., 2020; Hayter et al., 2007; Ramnani, 2006). Specifically, Crus I was recruited at both the domain level of Updating and at the paradigm-specific analyses. This area exhibits connectivity with higher-order processing areas, including the prefrontal, posterior-parietal, cingulate and parahippocampal areas in feedback loops (Schmahmann, 2019; Stoodley and Schmahmann, 2009). All Updating tasks also recruited cerebellar lobule VI, which has also been associated with working memory and language functions, potentially signaling a role for the cerebellum in verbal working memory (Stoodley and Schmahmann, 2009). Noticeably, our findings support previous evidence from patients with cerebellar lesions showing that the cerebellum is critical for working memory but not for other executive functions (Beuriat et al., 2020).

The consistent recruitment of cerebellar regions in the analyses relating to Updating addresses the longstanding question of whether the cerebellum plays a role in working memory. This in turn has important implications for studies targeting cerebellar functions. While traditionally the cerebellum was often considered a “motor” region, mounting evidence has demonstrated that cognitive, perceptual, and motor functions are supported by cerebellar activation (King et al., 2019; Schmahmann et al., 2019; Sokolov et al., 2017; Stoodley and Schmahmann, 2009). Additionally, cerebellar stimulation protocols may also affect cognitive functions (Hardwick et al., 2021).

Remarkably, through paradigm-specific analyses we distinguished the neural networks of Manipulation, N-back and Recognition paradigms. By definition, working memory refers to a system to maintain and manipulate information in the absence of external input. According to the multicomponent working memory model proposed by Baddeley and Hitch (1974), the system comprises modules to store sensorial information (loops) and a central executive to coordinate the content from the loops. The term working memory is frequently used for paradigms that specifically target the storage system (e.g., Sternberg task). To our knowledge, the first and last meta-analytical study to target the distinction between paradigms from the different modules of Baddeley and Hitch’s model was performed by Wager and Smith (2003). These authors observed greater increases in ventral and anterior prefrontal regions in manipulation paradigms. Our study did not replicate these findings, possibly due to the limited number of studies and a different meta-analytic technique used in the former publication. In our study, we found that the N-back and Manipulation tasks (which tackle the executive component) showed a high degree of overlap across fronto-parietal regions, insula and cerebellum, but only the N-back exhibited recruitment of the basal ganglia. The Recognition subdomain (storage component) showed a more distributed pattern across the fronto-parietal network, which covered the task networks of Manipulation and most of the N-back network in cortical regions. In comparison to Recognition, the N-back (but not Manipulation) subdomain showed activation in the right thalamus, the right caudate and a medial portion of cerebellar Crus I. Notably, the thalamus has been identified as an important hub that integrates information from different cortical networks (Hwang et al., 2017). Importantly, although all Updating paradigms recruited the right cerebellum (Lobule VI), only the left cerebellum (Lobule VII) showed activation in the Manipulation and N-back subdomains (executive module), but not in Recognition (storage module). This highlights the role of particular subcortical regions and left cerebellum in the manipulation of short-term stored information. Remarkably, this is supported by the impaired manipulation of visual representations in patients with degenerative cerebellar disorders (McDougle et al., 2022). The manipulation of stored information requires the system to switch among different ongoing cognitive processes. As observed in the previous section, Switching processing seems dominant in the left hemisphere. Therefore, it is possible that the activation of the left cerebellum during manipulation paradigms relates to dynamic cognitive demands from working memory, referred to as the executive module in the multicomponent working memory model.

In regard to the basal ganglia, the N-back subdomain showed to engage the caudate head whereas the Recognition subdomain recruited the caudate and the putamen. These activations overlap with different portions of basal ganglia activation from the Response inhibition tasks (Go/No-go and Stop Signal). Guo et al. (2018) showed that basal ganglia are involved in motor response inhibition and the suppression of thoughts. During the N-back and Recognition paradigms, it is crucial to maintain and update the relevant content while suppressing distracting information and this may possibly be the source of this neural commonality.

Overall, these results show that the different Updating subdomains present a widespread cortical activation pattern which partially overlaps with those from Inhibition and Shifting. Furthermore, our findings highlight the distinguishable role of the thalamus, basal ganglia and different regions of the cerebellum in paradigms that target distinct modules of the multicomponent working memory model.

4.5. *General discussion*

This study supports the unity-diversity model of Executive Functions (Miyake et al., 2000). The neural convergences across the three main executive domains consist of a canonical fronto-parietal network which, generically speaking, is considered to be engaged in a wide range of higher cognitive abilities (‘multiple demands network’, see Duncan 2010) that shares the coordination of different cognitive processes. This is in accordance with the definition of executive functions, which are the abilities that orchestrate different cognitive processes and behavior.

The general maps of each of the three main executive domains (Inhibition, Shifting and Updating) showed a substantial overlap with the ‘global’ executive network, which is not surprising as these analyses incorporate different types of paradigms from the same domain.

For the first time, we present intra-domain conjunction analyses. This approach allows us to override the frequent meta-analysis bias of maps mostly representing the most frequently used paradigms within each domain, and thus showing brain areas that may not be representative of all paradigms. Accordingly, our approach allows a more reliable identification of what is specifically distinctive for each domain and the consequent comparison between domains, thus providing a more differentiated perspective on brain activations associated with different domains of executive functioning than previous meta-analyses.

When looking at the commonalities among paradigms from the same domain (intra-domain conjunctions), Shifting and Inhibition are shown to be considerably distinct from each other and to be lateralized to the right and left hemispheres, respectively. In contrast, the networks of both the Shifting and Inhibition domains overlap with that from Updating. In addition to the intra-domain commonalities, we observe regions that are common between tasks from different domains while occasionally being inconsistent at intra-domain level. Thus, although there appears a quite distinct pattern of functional activation for each domain, the domain constructs do not seem entirely independent from a brain activity perspective.

This speaks to the neural signature of the general notion of unity and diversity of executive functions, as observed in behavioral studies and insights obtained from the study of brain damaged patients (Friedman and Robbins, 2022; Miyake and Friedman, 2012).

Accordingly, the maps from the intra-domain analyses, as well as those from the contrast analyses, should not be considered as being exclusive for that particular domain. Rather, these regions should be considered to be more relevant for (as compared to the other domains; contrast) or characteristic to a certain domain (as being recruited by all the paradigms from that domain; intra-domain).

We also present the activation maps of the most commonly used executive paradigms which allows their comparison at intra-domain as well as across-domain level. We notice reasonable consistency across paradigms for Updating and Shifting, but to a lesser extent for Inhibition. However, when regrouping the Inhibition paradigms into Response Inhibition and Interference Control, a more consistent pattern emerged.

The extensiveness of our endeavor provides robust evidence regarding the neural substrates of executive functions, executive domains (Inhibition, Shifting and Updating) and the most commonly used paradigms in experimental and clinical settings. The paradigm-specific analyses highlight that executive functions—despite their unity—are diverse and should therefore be treated as dissimilar aspects of cognitive functioning, also from a neuroimaging perspective.

Finally, across this manuscript we have used the term ‘network’ to refer to the maps resulting from our analyses under the assumption that the consistent co-activation of regions suggests some degree of interaction among the components. However, we did not execute connectivity analyses. As such, our interpretation of the interactions among the different regions of the network remains limited and is only discussed in light of previous literature. Previous meta-analytic work has focused on the dynamics of executive components at rest and during task performance (Camilleri et al., 2018). When comparing the present work with previous network analyses it is important to consider that some topographical inconsistency has been found among putative executive networks under similar names (e.g. central executive network, cognitive control network, executive network, frontoparietal network, etc.) (Witt et al., 2021). This may be due in part to the conceptual and neural overlap among different higher order systems (e.g., attention control, fluid intelligence, multiple-demand, etc.), as already discussed, and to the existence of executive sub-networks.

4.6. *Implications for behavior*

Our findings may have several implications for behavior. First, the convergence and divergence observed from the comparisons within and across domains may underlie the effects of near or far transfer in cognitive training interventions. Plausibly, the training of one domain or paradigm may effectively transfer to the improvement of other cognitive processes that share larger neural substrates (see Nguyen et al. 2019). It is anticipated that the transfer effects may be different across development as the neural commonalities and discrepancies among executive domains change with aging (Diamond, 2013; Heckner et al., 2021; Zhang et al., 2021).

Second, the comparison of different paradigms within each domain reveals heterogeneities that may underlie selective impairments in different clinical conditions. Whereas diverse psychiatric disorders have been characterized by deficits in the same domain (e.g. Shifting), the manifestation of these deficits may be different in each disorder. For instance, lack of flexibility is differentially expressed in autism, obsessive-compulsive disorder and ADHD (Uddin, 2021).

Third, in spite of the divergences, our intra-domain analyses reveal the core neural convergence of the different paradigms within each domain. Although this neural signature does not overlap between Inhibition and Shifting, both domains share a considerable overlap with Updating. It is worthy to mention that executive paradigms rarely involve one domain. Accordingly, failing in a particular task (e.g. N-back) could actually be due to problems in another domain (e.g. Inhibition) than the domain that is being targeted (in this case Updating) (Diamond, 2013). To this regard, empirical evidence from behavioral studies supports that the cognitive demands of working memory overlap with those from inhibition (Hasher et al., 1999; Bissett et al., 2021). Understanding how the different paradigms compare to each other within and across domains, may help to better understand behavioral interactions and deficits. Altogether, these insights may inspire the refinement of neuropsychological batteries and the customization of cognitive training and neurorehabilitation interventions.

4.7. *Neuroimaging, replicability, and publication bias*

Ongoing work has highlighted several issues with the robustness and replicability of scientific research (Nosek et al., 2022). This discussion is highly relevant to functional neuroimaging studies. The inherent costs of neuroimaging typically limit the sample sizes in a given study; consequently, individual neuroimaging studies often have low statistical power, which can increase the likelihood of both Type I and II errors (Button et al., 2013). Meta-analytic approaches such as ALE offer a solution to this limitation; pooling data across multiple studies effectively increases the total sample size, reduces the likelihood that study-specific noise will drive effects observed in the overall sample, and increases the likelihood that truly consistent effects across studies will be recognized.

Publication bias is also a source of concern for meta-analytic studies (Lin and Chu, 2018). This includes not only issues related to small sample sizes as discussed above, but also the further issue of the potential omission of null findings in the published literature. Although neuroimaging studies are not exempt from these biases, the norm is that researchers report all activation coordinates in a given study, which may or may not support their initial hypotheses. Furthermore, the inclusion of null results would not affect the ALE meta-analysis algorithm as used in the present study, as it depends critically on clustering of spatial coordinates across studies at a level above chance (Rottschy et al., 2012). This is notably different from traditional meta-analytic techniques that look to pool effect sizes across studies; as such, it has been argued that coordinate-based meta-analyses may be less susceptible to this form of publication bias (Rottschy et al., 2012). While a hypothetical scenario exists whereby studies are not published if they fail to identify activations in a pre-specified region, prior research indicates that this proposed effect does not drive publication bias in neuroimaging (Jennings and van Horn, 2012).

In summary, coordinate-based meta-analysis approaches such as ALE provide a useful approach to address the typically limited sample sizes found in the neuroimaging literature. ALE meta-analysis therefore provides a quantitative synthesis of the results in a given field, and while the coordinate-based approach of ALE makes it relatively robust to issues that affect traditional effect-size meta-analysis techniques, results should still be considered as a reflection of the available literature rather than ‘absolute truths’.

5. Conclusions

In our comprehensive meta-analysis on executive functions, we identified a common executive network that involves fronto-parietal and subcortical areas. Intra-domain conjunction analyses revealed a considerable distinction between Shifting and Inhibition, including marked lateralization to the right and left hemispheres, respectively, while both networks overlap with that from Updating. Thus, while distinct patterns of functional activation emerged for each domain, the domain constructs do not seem entirely independent from a brain activity perspective. This supports the notion of unity and diversity of executive functions (Friedman and Robbins, 2022; Miyake and Friedman, 2012). Paradigm-level analyses suggest that Inhibition paradigms should be grouped into Response Inhibition and Interference Control tasks. Since executive functioning constitutes dynamic processes evolving across distributed brain areas, future analyses should consider using connectivity meta-analytic approaches to shed light on the distinctive dynamic properties of task-related executive functioning networks.

Data and code availability statement

The individual reports of the studies included in the global analyses and in each category (domains and subdomains), the Matlab codes and resulting NIfTI files can be consulted at: https://osf.io/d85pb/?view_only=f0b3fcad577d4ff39cb4e6f3cd34e63f.

Ethics statement

There were no ethical concerns on this study as no original data was directly acquired from the authors.

Declaration of Competing Interest

The authors declare no conflicts of interest.

Credit authorship contribution statement

Geraldine Rodríguez-Nieto: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Project administration, Visualization, Writing – original draft, Writing – review & editing. **Caroline Seer:** Conceptualization, Methodology, Validation, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration, Funding acquisition. **Justina Sidlauskaite:** Investigation. **Lore Vleugels:** Investigation. **Anke Van Roy:** Investigation. **Robert Hardwick:** Conceptualization, Methodology, Software, Validation, Formal analysis, Data curation, Writing – original draft, Writing – review & editing, Visualization, Supervision, Funding acquisition. **Stephan Swinnen:** Conceptualization, Writing – review & editing, Resources, Supervision, Funding acquisition.

Data Availability

We have made our data available and provided the link to the repository.

Acknowledgements

Funding was provided by: KU Leuven Research Fund (C16/15/070) to SS; the Fonds Wetenschappelijk Onderzoek – Vlaanderen (FWO) (G089818N) to SS; the Excellence of Science (EOS) grant from FWO and the Fonds de la Recherche Scientifique (FNRS) (EOS 30446199, MEMODYN) to SS; UC Louvain special research fund (1C.21300.057 and 1C.21300.058) to RH; the European Union's Horizon 2020 – Marie Skłodowska-Curie grant (794042) to CS; a postdoctoral fellowship from the FWO (179732) to CS; and FNRS research fellowship (1C.21300.0580) to LV.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2022.119665.

References

Ardila, A., Bernal, B., Rosselli, M., 2018. Executive functions brain system: an activation likelihood estimation meta-analytic study. Arch. Clin. Neuropsychol. 33 (4), 379–405.

Aron, A.R., Robbins, T.W., Poldrack, R.A., 2014. Inhibition and the right inferior frontal cortex: one decade on. Trends Cogn. Sci. 18 (4), 177–185. doi:10.1016/j.tics.2013.12.003.

Baddeley, A.D., 2012. Working memory: theories, models, and controversies. Annu. Rev. Psychol. 63 (1), 1–29. doi:10.1146/annurev-psych-120710-100422.

Baddeley, A.D., Hitch, G., 1974. Working memory. In: Psychology of Learning and Motivation, 8. Elsevier, pp. 47–89. doi:10.1016/S0079-7421(08)60452-1.

Baddeley, A.D., Hitch, G.J., 1994. Developments in the concept of working memory. Neuropsychology 8 (4), 485–493. doi:10.1037/0894-4105.8.4.485.

Beissner, F., Meissner, K., Bar, K.J., Napadow, V., 2013. The autonomic brain: an activation likelihood estimation meta-analysis for central processing of autonomic function. J. Neurosci. 33 (25), 10503–10511. doi:10.1523/JNEUROSCI.1103-13.2013.

Beuriat, P.A., Cohen-Zimerman, S., Smith, G.N.L., Krueger, F., Gordon, B., Grafman, J., 2020. A new insight on the role of the cerebellum for executive functions and emotion processing in adults. Front. Neurol. 11, 593490. doi:10.3389/fneur.2020.593490.

Bissett, P., Jones, H.M., Hagen, M.P., Bui, T.T.T., Li, J., Shine, J.M., Poldrack, R., 2021. Towards a taxonomy of inhibition-related processes: a dual-task approach. PsyArXiv doi:10.31234/osf.io/spfyu.

Bonifazi, P., Erramuzpe, A., Diez, I., Gabilondo, I., Boisgontier, M.P., Pauwels, L., Stramaglia, S., Swinnen, S.P., Cortes, J.M., 2018. Structure–function multi-scale connectomics reveals a major role of the fronto-striato-thalamic circuit in brain aging. Hum. Brain Mapp. 39 (12), 4663–4677. doi:10.1002/hbm.24312.

Brass, M., Derrfuss, J., Forstmann, B., Cramon, D., 2005. The role of the inferior frontal junction area in cognitive control. Trends Cogn. Sci. 9 (7), 314–316. doi:10.1016/j.tics.2005.05.001.

Button, K.S., Ioannidis, J., Mokrysz, C., Nosek, B.A., Flint, J., Robinson, E.S., Munafò, M.R., 2013. Power failure: why small sample size undermines the reliability of neuroscience. Nat. Rev. Neurosci. 14 (5), 365–376. doi:10.1038/nrn3475.

Cai, W., Ryali, S., Chen, T., Li, C.S.R., Menon, V., 2014. Dissociable roles of right inferior frontal cortex and anterior insula in inhibitory control: evidence from intrinsic and task-related functional parcellation, connectivity, and response profile analyses across multiple datasets. J. Neurosci. 34 (44), 14652–14667. doi:10.1523/JNEUROSCI.3048-14.2014.

Camilleri, J.A., Müller, V.I., Fox, P., Laird, A.R., Hoffstaedter, F., Kalenscher, T., Eickhoff, S.B., 2018. Definition and characterization of an extended multiple-demand network. NeuroImage 165, 138–147 1.

Chase, H.W., Eickhoff, S.B., Laird, A.R., Hogarth, L., 2011. The neural basis of drug stimulus processing and craving: an activation likelihood estimation meta-analysis. Biol. Psychiatry 70 (8), 785–793. doi:10.1016/j.biopsych.2011.05.025.

Cipolotti, L., Spanò, B., Healy, C., Tudor-Sfetea, C., Chan, E., White, M., Biondo, F., Duncan, J., Shallice, T., Bozzali, M., 2016. Inhibition processes are dissociable and lateralized in human prefrontal cortex. Neuropsychologia 93, 1–12. doi:10.1016/j.neuropsychologia.2016.09.018.

Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. Nat. Rev. Neurosci. 3 (3), 201–215. doi:10.1038/nrn755.

Coxon, J.P., Goble, D.J., Leunissen, I., Van Impe, A., Wenderoth, N., Swinnen, S.P., 2016. Functional brain activation associated with inhibitory control deficits in older adults. Cereb. Cortex 26 (1), 12–22. doi:10.1093/cercor/bhu165.

Criaud, M., Boulinguez, P., 2013. Have we been asking the right questions when assessing response inhibition in go/no-go tasks with fMRI? A meta-analysis and critical review. Neurosci. Biobehav. Rev. 37 (1), 11–23. doi:10.1016/j.neubiorev.2012.11.003.

Cristofori, I., Cohen-Zimerman, S., Grafman, J., 2019. Executive functions. In: Handbook of Clinical Neurology, 163. Elsevier, pp. 197–219. doi:10.1016/B978-0-12-804281-6.00011-2.

Derrfuss, J., Brass, M., Neumann, J., von Cramon, D.Y., 2005. Involvement of the inferior frontal junction in cognitive control: meta-analyses of switching and Stroop studies. Hum. Brain Mapp. 25 (1), 22–34. doi:10.1002/hbm.20127.

Diamond, A., 2013. Executive functions. Annu. Rev. Psychol. 64 (1), 135–168. doi:10.1146/annurev-psych-113011-143750.

Duncan, J., 2010. The multiple-demand (MD) system of the primate brain: mental programs for intelligent behaviour. Trends Cogn. Sci. 14 (4), 172–179.

Eickhoff, S.B., Bzdok, D., Laird, A.R., Kurth, F., Fox, P.T., 2012. Activation likelihood estimation meta-analysis revisited. NeuroImage 59 (3), 2349–2361. doi:10.1016/j.neuroimage.2011.09.017.

Eickhoff, S.B., Heim, S., Zilles, K., Amunts, K., 2006. Testing anatomically specified hypotheses in functional imaging using cytoarchitectonic maps. NeuroImage 32 (2), 570–582. doi:10.1016/j.neuroimage.2006.04.204.

Eickhoff, S.B., Laird, A.R., Grefkes, C., Wang, L.E., Zilles, K., Fox, P.T., 2009. Coordinate-based activation likelihood estimation meta-analysis of neuroimaging data: a random-effects approach based on empirical estimates of spatial uncertainty. Hum. Brain Mapp. 30 (9), 2907–2926. doi:10.1002/hbm.20718.

Eickhoff, S.B., Nichols, T.E., Laird, A.R., Hoffstaedter, F., Amunts, K., Fox, P.T., Bzdok, D., Eickhoff, C.R., 2016. Behavior, sensitivity, and power of activation likelihood estimation characterized by massive empirical simulation. NeuroImage 137, 70–85. doi:10.1016/j.neuroimage.2016.04.072.

Eickhoff, S.B., Paus, T., Caspers, S., Grosbras, M.H., Evans, A.C., Zilles, K., Amunts, K., 2007. Assignment of functional activations to probabilistic cytoarchitectonic areas revisited. NeuroImage 36 (3), 511–521. doi:10.1016/j.neuroimage.2007.03.060.

Eickhoff, S.B., Stephan, K.E., Mohlberg, H., Grefkes, C., Fink, G.R., Amunts, K., Zilles, K., 2005. A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. NeuroImage 25 (4), 1325–1335. doi:10.1016/j.neuroimage.2004.12.034.

Erickson, L.C., Heeg, E., Rauschecker, J.P., Turkeltaub, P.E., 2014. An ALE meta-analysis on the audiovisual integration of speech signals: ALE meta-Analysis on AV speech Integration. Hum. Brain Mapp. 35 (11), 5587–5605. doi:10.1002/hbm.22572.

Erika-Florence, M., Leech, R., Hampshire, A., 2014. A functional network perspective on response inhibition and attentional control. Nat. Commun. 5 (1), 4073. doi:10.1038/ncomms5073.

Evans, A.C., Kamber, M., Collins, D.L., MacDonald, D., Shorvon, S.D., Fish, D.R., Andermann, F., Bydder, G.M., Stefan, H., 1994. An MRI-based probabilistic atlas of neuroanatomy. In: Magnetic Resonance Scanning and Epilepsy. Springer US, pp. 263–274. doi:10.1007/978-1-4615-2546-2_48.

Fedorenko, E., Duncan, J., Kanwisher, N., 2013. Broad domain generality in focal regions of frontal and parietal cortex. Proc. Natl. Acad. Sci. 110 (41), 16616–16621. doi:10.1073/pnas.1315235110.

Florio, T.M., Scarnati, E., Rosa, I., Di Censo, D., Ranieri, B., Cimini, A., Galante, A., Alecci, M., 2018. The basal ganglia: more than just a switching device. CNS Neurosci. Therapeut. 24 (8), 677–684. doi:10.1111/cns.12987.

Friedman, N.P., Miyake, A., 2004. The relations among inhibition and interference control functions: a latent-variable analysis. J. Exp. Psychol. Gen. 133 (1), 101–135. doi:10.1037/0096-3445.133.1.101.

Friedman, N.P., Miyake, A., 2017. Unity and diversity of executive functions: individual differences as a window on cognitive structure. Cortex 86, 186–204. doi:10.1016/j.cortex.2016.04.023.

Friedman, N.P., Robbins, T.W., 2022. The role of prefrontal cortex in cognitive control and executive function. Neuropsychopharmacology 47 (1), 72–89. doi:10.1038/s41386-021-01132-0.

Guo, Y., Schmitz, T.W., Mur, M., Ferreira, C.S., Anderson, M.C., 2018. A supramodal role of the basal ganglia in memory and motor inhibition: meta-analytic evidence. Neuropsychologia 108, 117–134. doi:10.1016/j.neuropsychologia.2017.11.033.

Gustavson, D.E., Panizzon, M.S., Franz, C.E., Reynolds, C.A., Corley, R.P., Hewitt, J.K., Lyons, M.J., Kremen, W.S., Friedman, N.P., 2019. Integrating verbal fluency with executive functions: evidence from twin studies in adolescence and middle age. J. Exp. Psychol. Gen. 148 (12), 2104–2119. doi:10.1037/xge0000589, Link to external site, this link will open in a new window.

Hagmann, P., Cammoun, L., Gigandet, X., Meuli, R., Honey, C.J., Wedeen, V.J., Sporns, O., 2008. Mapping the structural core of human cerebral cortex. PLOS Biol. 6 (7), e159. doi:10.1371/journal.pbio.0060159.

Hannah, R., Aron, A.R., 2021. Towards real-world generalizability of a circuit for action-stopping. Nat. Rev. Neurosci. 22 (9), 538–552.

Hardwick, R.M., Therrien, A.S., Lesage, E., 2021. Non-invasive stimulation of the motor cerebellum has potential cognitive confounds. Brain Stimul. 14 (4), 922–923. doi:10.1016/j.brs.2021.05.011.

Hasher, L., Zacks, R.T., May, C.P., Gopher, D., Koriat, A., 1999. Inhibitory control, circadian arousal, and age. In: Attention and Performance, XVII, Cognitive Regulation of Performance: Interaction of Theory and Application. MIT Press, Cambridge, MA, pp. 653–675.

Hayter, A.L., Langdon, D.W., Ramnani, N., 2007. Cerebellar contributions to working memory. NeuroImage 36 (3), 943–954. doi:10.1016/j.neuroimage.2007.03.011.

Heckner, M.K., Cieslik, E.C., Eickhoff, S.B., Camilleri, J.A., Hoffstaedter, F., Langner, R., 2021. The aging brain and executive functions revisited: implications from meta-analytic and functional-connectivity evidence. J. Cogn. Neurosci. 33 (9), 1716–1752. doi:10.1162/jocn_a_01616.

Hedden, T., Yoon, C., 2006. Individual differences in executive processing predict susceptibility to interference in verbal working memory. Neuropsychology 20 (5), 511.

Huang, Y., Su, L., Ma, Q., 2020. The stroop effect: an activation likelihood estimation meta-analysis in healthy young adults. Neurosci. Lett. 716, 134683. doi:10.1016/j.neulet.2019.134683.

Hung, Y., Gaillard, S.L., Yarmak, P., Arsalidou, M., 2018. Dissociations of cognitive inhibition, response inhibition, and emotional interference: voxelwise ALE meta-analyses of fMRI studies. Hum. Brain Mapp. 39 (10), 4065–4082. doi:10.1002/hbm.24232.

Hwang, K., Bertolero, M.A., Liu, W.B., D'Esposito, M., 2017. The human thalamus is an integrative hub for functional brain networks. J. Neurosci. 37 (23), 5594–5607. doi:10.1523/JNEUROSCI.0067-17.2017.

Jennings, R.G., Van Horn, J.D., 2012. Publication bias in neuroimaging research: implications for meta-analyses. Neuroinformatics 10 (1), 67–80.

Kane, M.J., Engle, R.W., 2002. The role of prefrontal cortex in working-memory capacity, executive attention, and general fluid intelligence: an individual-differences perspective. Psychon. Bull. Rev. 9 (4), 637–671.

King, M., Hernandez-Castillo, C.R., Poldrack, R.A., Ivry, R.B., Diedrichsen, J., 2019. Functional boundaries in the human cerebellum revealed by a multi-domain task battery. Nat. Neurosci. 22 (8), 1371–1378. doi:10.1038/s41593-019-0436-x.

Koch, I., Poljac, E., Müller, H., Kiesel, A., 2018. Cognitive structure, flexibility, and plasticity in human multitasking—an integrative review of dual-task and task-switching research. Psychol. Bull. 144 (6), 557–583. doi:10.1037/bul0000144.

Lancaster, J.L., Tordesillas-Gutiérrez, D., Martinez, M., Salinas, F., Evans, A., Zilles, K., Mazziotta, J.C., Fox, P.T., 2007. Bias between MNI and Talairach coordinates analyzed using the ICBM-152 brain template. Hum. Brain Mapp. 28 (11), 1194–1205. doi:10.1002/hbm.20345.

Langner, R., Eickhoff, S.B., 2013. Sustaining attention to simple tasks: a meta-analytic review of the neural mechanisms of vigilant attention. Psychol. Bull. 139 (4), 870–900. doi:10.1037/a0030694.

Lemire-Rodger, S., Lam, J., Viviano, J.D., Stevens, W.D., Spreng, R.N., Turner, G.R., 2019. Inhibit, switch, and update: a within-subject fMRI investigation of executive control. Neuropsychologia 132, 107134.

Lin, L., Chu, H., 2018. Quantifying publication bias in meta-analysis. Biometrics 74 (3), 785–794. doi:10.1111/2Fbiom.12817.

Luo, Z., Zeng, L.L., Qin, J., Hou, C., Shen, H., Hu, D., 2020. Functional parcellation of human brain precuneus using density-based clustering. Cereb. Cortex 30 (1), 269–282. doi:10.1093/cercor/bhz086.

Mayka, M.A., Corcos, D.M., Leurgans, S.E., Vaillancourt, D.E., 2006. Three-dimensional locations and boundaries of motor and premotor cortices as defined by functional brain imaging: a meta-analysis. NeuroImage 31 (4), 1453–1474. doi:10.1016/j.neuroimage.2006.02.004.

McDougle, S.D., Tsay, J., Pitt, B., King, M., Saban, W., Taylor, J.A., Ivry, R.B., 2022. Continuous manipulation of mental representations is compromised in cerebellar degeneration. Brain Feb 24, awac072. doi:10.1093/brain/awac072.

Miller, E.K., Cohen, J.D., 2001. An integrative theory of prefrontal cortex function. Annu. Rev. Neurosci. 24 (1), 167–202. doi:10.1146/annurev.neuro.24.1.167.

Miyake, A., Friedman, N.P., 2012. The nature and organization of individual differences in executive functions: four general conclusions. Curr. Dir. Psychol. Sci. 21 (1), 8–14. doi:10.1177/0963721411429458.

Miyake, A., Friedman, N.P., Emerson, M.J., Witzki, A.H., Howerter, A., Wager, T.D., 2000. The unity and diversity of executive functions and their contributions to complex "frontal lobe" tasks: a latent variable analysis. Cogn. Psychol. 41 (1), 49–100. doi:10.1006/cogp.1999.0734.

Muhle-Karbe, P.S., Derrfuss, J., Lynn, M.T., Neubert, F.X., Fox, P.T., Brass, M., Eickhoff, S.B., 2016. Co-activation-based parcellation of the lateral prefrontal cortex delineates the inferior frontal junction area. Cereb. Cortex 26 (5), 2225–2241. doi:10.1093/cercor/bhv073.

Müller, V.I., Langner, R., Cieslik, E.C., Rottschy, C., Eickhoff, S.B., 2015. Interindividual differences in cognitive flexibility: influence of gray matter volume, functional connectivity and trait impulsivity. Brain Struct. Funct. 220 (4), 2401–2414. doi:10.1007/s00429-014-0797-6.

Nee, D.E., Wager, T.D., Jonides, J., 2007. Interference resolution: insights from a meta–analysis of neuroimaging tasks. Cogn. Affect. Behav. Neurosci. 7 (1), 1–17.

Nguyen, L., Murphy, K., Andrews, G., 2019. Cognitive and neural plasticity in old age: a systematic review of evidence from executive functions cognitive training. Ageing Res. Rev. 53, 100912. doi:10.1016/j.arr.2019.100912.

Nichols, T., Brett, M., Andersson, J., Wager, T., Poline, J.B., 2005. Valid conjunction inference with the minimum statistic. NeuroImage 25 (3), 653–660. doi:10.1016/j.neuroimage.2004.12.005.

Niendam, T.A., Laird, A.R., Ray, K.L., Dean, Y.M., Glahn, D.C., Carter, C.S., 2012. Meta-analytic evidence for a superordinate cognitive control network subserving diverse executive functions. Cogn. Affect. Behav. Neurosci. 12 (2), 241–268. doi:10.3758/s13415-011-0083-5.

Nigg, J.T., 2000. On inhibition/disinhibition in developmental psychopathology: views from cognitive and personality psychology and a working inhibition taxonomy. Psychol. Bull. 126 (2), 220.

Nosek, B.A., Hardwicke, T.E., Moshontz, H., Allard, A., Corker, K.S., Dreber, A., Vazire, S., 2022. Replicability, robustness, and reproducibility in psychological science. Annu. Rev. Psychol. 73 (1), 719–748. doi:10.1146/annurev-psych-020821-114157.

Rae, C.L., Hughes, L.E., Weaver, C., Anderson, M.C., Rowe, J.B., 2014. Selection and stopping in voluntary action: a meta-analysis and combined fMRI study. NeuroImage 86, 381–391. doi:10.1016/j.neuroimage.2013.10.012.

Ramnani, N., 2006. The primate cortico-cerebellar system: anatomy and function. Nat. Rev. Neurosci. 7 (7), 511–522. doi:10.1038/nrn1953.

Rottschy, C., Langner, R., Dogan, I., Reetz, K., Laird, A.R., Schulz, J.B., Fox, P.T., Eickhoff, S.B., 2012. Modelling neural correlates of working memory: a coordinate-based meta-analysis. NeuroImage 60 (1), 830–846. doi:10.1016/j.neuroimage.2011.11.050.

Schmahmann, J.D., 2019. The cerebellum and cognition. Neurosci. Lett. 688, 62–75. doi:10.1016/j.neulet.2018.07.005.

Schmahmann, J.D., Guell, X., Stoodley, C.J., Halko, M.A., 2019. The theory and neuroscience of cerebellar cognition. Annu. Rev. Neurosci. 42 (1), 337–364. doi:10.1146/annurev-neuro-070918-050258.

Sebastian, A., Jung, P., Neuhoff, J., Wibral, M., Fox, P.T., Lieb, K., Fries, P., Eickhoff, S.B., Tüscher, O., Mobascher, A., 2016. Dissociable attentional and inhibitory networks of dorsal and ventral areas of the right inferior frontal cortex: a combined task-specific and coordinate-based meta-analytic fMRI study. Brain Struct. Funct. 221 (3), 1635–1651. doi:10.1007/s00429-015-0994-y.

Sebastian, A., Konken, A.M., Schaum, M., Lieb, K., Tüscher, O., Jung, P., 2021. Surprise: unexpected action execution and unexpected inhibition recruit the same fronto-basal-ganglia network. J. Neurosci. 41 (11), 2447–2456. doi:10.1523/JNEUROSCI.1681-20.2020.

Seer, C., Sidlauskaite, J., Lange, F., Rodríguez-Nieto, G., Swinnen, S.P., 2021. Cognition and action: a latent variable approach to study contributions of executive functions to motor control in older adults. Aging 13 (12), 15942–15963. doi:10.18632/aging.203239.

Sokolov, A.A., Miall, R.C., Ivry, R.B., 2017. The cerebellum: adaptive prediction for movement and cognition. Trends Cogn. Sci. 21 (5), 313–332. doi:10.1016/j.tics.2017.02.005.

Song, P., Lin, H., Liu, C., Jiang, Y., Lin, Y., Xue, Q., Xu, P., Wang, Y., 2019. Transcranial magnetic stimulation to the middle frontal gyrus during attention modes induced dynamic module reconfiguration in brain networks. Front. Neuroinform. 13, 22. doi:10.3389/fninf.2019.00022.

Stoodley, C., Schmahmann, J., 2009. Functional topography in the human cerebellum: a meta-analysis of neuroimaging studies. NeuroImage 44 (2), 489–501. doi:10.1016/j.neuroimage.2008.08.039.

Stuss, D.T., 2011. Functions of the frontal lobes: relation to executive functions. J. Int. Neuropsychol. Soc. 17 (05), 759–765. doi:10.1017/S1355617711000695.

Sullivan, J.R., Riccio, C.A., Castillo, C.L., 2009. Concurrent validity of the tower tasks as measures of executive function in adults: a meta-analysis. Appl. Neuropsychol. 16 (1), 62–75. doi:10.1080/09084280802644243.

Swick, D., Ashley, V., Turken, U., 2011. Are the neural correlates of stopping and not going identical? Quantitative meta-analysis of two response inhibition tasks. NeuroImage 56 (3), 1655–1665. doi:10.1016/j.neuroimage.2011.02.070.

Turkeltaub, P.E., Eden, G.F., Jones, K.M., Zeffiro, T.A., 2002. Meta-analysis of the functional neuroanatomy of single-word reading: method and validation. NeuroImage 16 (3), 765–780. doi:10.1006/nimg.2002.1131.

Turkeltaub, P.E., Eickhoff, S.B., Laird, A.R., Fox, M., Wiener, M., Fox, P., 2012. Minimizing within-experiment and within-group effects in activation likelihood estimation meta-analyses. Brain Mapp. 33 (1), 1–13. doi:10.1002/hbm.21186.

Uddin, L.Q., 2021. Cognitive and behavioural flexibility: neural mechanisms and clinical considerations. Nat. Rev. Neurosci. 22 (3), 167–179. doi:10.1038/s41583-021-00428-w.

Wager, T.D., Jonides, J., Reading, S., 2004. Neuroimaging studies of shifting attention: a meta-analysis. Neuroimage 22 (4), 1679–1693.

Wager, T.D., Smith, E.E., 2003. Neuroimaging studies of working memory. Cogn. Affect. Behav. Neurosci. 3 (4), 255–274.

Wager, T.D., Sylvester, C.Y.C., Lacey, S.C., Nee, D.E., Franklin, M., Jonides, J., 2005. Common and unique components of response inhibition revealed by fMRI. NeuroImage 27 (2), 323–340. doi:10.1016/j.neuroimage.2005.01.054.

Wang, J., Yang, Y., Fan, L., Xu, J., Li, C., Liu, Y., Fox, P.T., Eickhoff, S.B., Yu, C., Jiang, T., 2015. Convergent functional architecture of the superior parietal lobule unraveled with multimodal neuroimaging approaches: parcellation of superior parietal lobule. Hum. Brain Mapp. 36 (1), 238–257. doi:10.1002/hbm.22626.

Weiner, K.S., Zilles, K., 2016. The anatomical and functional specialization of the fusiform gyrus. Neuropsychologia 83, 48–62. doi:10.1016/j.neuropsychologia.2015.06.033.

Wessel, J.R., Aron, A.R., 2017. On the Globality of motor suppression: unexpected events and their influence on behavior and cognition. Neuron 93 (2), 259–280. doi:10.1016/j.neuron.2016.12.013.

Wijeakumar, S., Magnotta, V.A., Buss, A.T., Ambrose, J.P., Wifall, T.A., Hazeltine, E., Spencer, J.P., 2015. Response control networks are selectively modulated by attention to rare events and memory load regardless of the need for inhibition. NeuroImage 120, 331–344. doi:10.1016/j.neuroimage.2015.07.026.

Witt, S.T., van Ettinger-Veenstra, H., Salo, T., Riedel, M.C., Laird, A.R., 2021. What executive function network is that? An image-based meta-analysis of network labels. Brain Topogr. 34 (5), 598–607.

Worringer, B., Langner, R., Koch, I., Eickhoff, S.B., Eickhoff, C.R., Binkofski, F.C., 2019. Common and distinct neural correlates of dual-tasking and task-switching: a meta-analytic review and a neuro-cognitive processing model of human multitasking. Brain Struct. Funct. 224 (5), 1845–1869. doi:10.1007/s00429-019-01870-4.

Wu, Y., Uluç, I., Schmidt, T.T., Tertel, K., Kirilina, E., Blankenburg, F., 2018. Overlapping frontoparietal networks for tactile and visual parametric working memory representations. NeuroImage 166, 325–334. doi:10.1016/j.neuroimage.2017.10.059.

Zhang, R., Geng, X., Lee, T.M.C., 2017. Large-scale functional neural network correlates of response inhibition: an fMRI meta-analysis. Brain Struct. Funct. 222 (9), 3973–3990. doi:10.1007/s00429-017-1443-x.

Zhang, Z., Peng, P., Eickhoff, S.B., Lin, X., Zhang, D., Wang, Y., 2021. Neural substrates of the executive function construct, age-related changes, and task materials in adolescents and adults: ALE meta-analyses of 408 fMRI studies. Dev. Sci. (6) 24. doi:10.1111/desc.13111.