Age-Related Changes in Executive Functions: Evidence from Coordinate-Based Meta-Analyses

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Abstract

Healthy aging is associated with altered behavioral performance and brain activation patterns on several cognitive tasks, especially tasks that emphasize high cognitive demands, such as executive functions. However, it remains unclear which regions and mechanisms underlie cognitive aging as the results of imaging studies vary considerably. The present study conducts activation likelihood estimation (ALE) meta-analyses to investigate age-related changes in executive functions and its subcomponents working memory, inhibition, and attention. The sample comprised a total of *n* = 43 experiments for working memory, *n* = 21 for inhibition, and *n* = 24 for attention. The meta-analyses revealed three regions affected by cognitive aging: the left IFJ, the right DLPFC, and the left V1. Age-related increased convergent activity in the left IFJ and V1, and decreased convergent activity in the right DLPFC was found. The findings suggest the IFJ to be a key region of executive functions, which is activated across tasks, stimuli, and subcomponents. Updating task representations and integrating spatial cognition, language, and memory may require more effort for older adults, which could explain the increased need to recruit the left IFJ. Age-related decreased convergence in the right DLPFC and increased convergence in the left V1, may represent an impairment of goal-maintenance and thus the need to recruit different neural circuits. Linking the results to existing cognitive aging theories, the results support the use of neural scaffolds in terms of greater activation and additional neural circuits in the aging brain.

Keywords: aging, executive functions, working memory, inhibition, attention, meta-analysis

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Executive Functions

Executive functions (EF), also called executive control or cognitive control, are a loosely defined set of cognitive skills and processes which appear critical for complex thought and behavior. The concept of EF is strongly influenced by observations of patients with frontal lobe lesions. Brain damage of the frontal lobe has been found to influence planning, organization, abstract thought, complex decision making, the regulation of emotion and impulses, the sequencing of goal-directed behavior, and the monitoring of action and thoughts (e.g. Mesulam, 2002). In line with these propositions, frontal lobe processes are described as top-down mental processes, which are important for non-automatic, non-impulsive, and non-instinctive behavior (Espy, 2004; Mesulam, 2002; Miller, & Cohen, 2001). It is suggested that their main function is to adapt to new or complex situations, when repetitive, overlearned cognitive abilities or behavior are no longer sufficient (Collette, Hogge, Salmon, & Van der Linden, 2006).

Among the first to describe EF were Baddeley and Hitch (1974) in their working memory model, consisting of three components: a modality-free central executive, which allows multitasking, shifting between tasks, selective attention, and the inhibition of irrelevant stimuli, the visuo-spatial sketch pad for the temporal keeping and manipulation of visual and spatial information, and the phonological loop for the temporal keeping and manipulation of linguistic information. Another important neuropsychological model that describes the control of information processing was proposed by Norman and Shallice (1982). It consists of two controlling systems: the contention scheduling, which activates schemata necessary to accomplish routine tasks, and the supervisory attentional system

(SAS), which is needed in novel or problematic situations. According to Baddeley (1986) the SAS can be seen as equivalent to the central executive in his model.

Despite the lack of a clear formal definition of EF, there is a relative agreement in terms of their complexity and importance for human adaptive behavior (Jurado, & Rosselli, 2007). For a long time the great question was whether EF represent one single or multiple fractioned processes. Baddeley (1996) proposed, based upon literature review, that the central executive is divided into four different functions: the capacity to assign resources during the simultaneous execution of two tasks, the capacity to adjust retrieval strategies, the capacity to selectively focus on one stimulus and inhibit the disrupting effect of others, and the capacity to keep and manipulate information stored in long-term memory. Missing intercorrelations between different tests for EF supported these proposals (Lehto, 1996). Thus, Lehto suggested separate subcomponents of EF, which disagrees with a unitary, single process. In 2000 Miyake, Friedman, Emerson, Witzki, and Howerter proposed three separate but not completely independent subcomponents of EF, based upon latent variable analysis: set shifting, working memory, and inhibition. Alvarez and Emory (2006) postulated three similar subcomponents: working memory, inhibition, and sustained and selective attention. Taking these findings into account, EF seem to be a macro-construct in which multiple EF subprocesses interact that enable complex thought and behavior. Regarding the discussion whether they are a single or a fractioned process, they might also be described as *unity AND diversity* (Friedman et al., 2016; Miyake et al., 2000; Teuber, 1972).

Neural Correlates of Executive Functions. For a long time, it was thought that EF were exclusively based in the frontal cortex as patients with frontal lesions often showed deficits in EF (Duncan, 1986; Owen, Downes, Sahakian, Polkey, & Robbins, 1990; Shallice, 1982). However, patients with frontal lesions can perform within a normal range on tests of EF (e.g. Eslinger & Damasio, 1985; Shallice, & Burgess, 1991) and patients with non-frontal lesions can show similar deficits as patients with frontal lesions (e.g. Anderson, Damasio, Jones, & Tranel, 1991; Axelrod et al., 1996; Mountain, & Snow-William, 1993). When frontal regions do not necessarily involve executive dysfunction and executive functioning is not exclusively based in frontal regions, EF seem to be based on a rather wide-spread network. This is in line with findings that show that executive deficits are often found in patients with diffuse lesions (Cowey, & Green, 1996; Simkins-Bullock, Brown, Greiffstein, Malik, & McGillicuddy, 1994).

So far there are substantial differences in the brain regions involved in different tasks found by neuroimaging studies investigating EF, which is partly due to the elusive concept of EF (Collette et al., 2006). There is widespread agreement that the prefrontal cortex (PFC) is a key region (e.g. Alvarez, & Emory, 2006; Buchsbaum, Greer, Chang, & Berman, 2005), but executive functioning depends on posterior regions as well (e.g. D'Esposito, & Grossman, 1996; Duncan, & Owen, 2000; Stuss, & Levine, 2002). Collette and Van der Linden (2002) found some prefrontal areas (dorsolateral prefrontal cortex [DLPFC], frontopolar PFC, and anterior cingulate gyrus [ACG]) that are systematically activated throughout a wide range of executive tasks, while other frontal and posterior areas are only activated in some tasks and thus might have a more specific function. Wager and Smith (2003) showed that different executive tasks are associated with specific cerebral areas, which is in line with neuropsychological theories proposing subcomponents of EF (e.g. Alvarez & Emory, 2006; Lehto, 1996; Miyake et al., 2000). In 2010 Duncan proposed a multiple-demand (MD) system, which was found to be consistently recruited in tasks with different cognitive demands. Müller, Langner, Cieslik, Rottschy and Eickhoff (2014) integrated results from three meta-analyses investigating working memory (Rottschy et al., 2012), attention (Langner, & Eickhoff, 2013), and inhibition (Cieslik, Müller, Eickhoff, Langner, & Eickhoff, 2013), the most discussed subcomponents of EF (Alvarez, & Emory, 2006; Miyake et al., 2000), to find a common core network in humans. They found a network of seven regions (middle cingulate cortex/supplementary motor area [MCC/SMA], bilateral inferior frontal junction/gyrus [IFJ/G], right middle frontal gyrus [MFG], bilateral anterior insula [aINS], right inferior parietal cortex [IPC], and intraparietal sulcus [IPS]) which is similar to the one Duncan found. In 2017 (manuscript) Camilleri and colleagues followed up on and expanded these findings. They proposed an extended multiple-demand network (eMDN) which is based on task-dependent and task-independent functional connectivity analyses seeded from the regions of the meta-analytically defined multiple-demand network by Müller and colleagues. They found 17 regions (bilateral IFJ, aINS, SMA, pre-SMA, IPS, Putamen, Thalamus, right MFG extending into the inferior frontal sulcus [IFS], left dorsal pre-motor cortex [dPMC], and inferior temporal gyrus [ITG]). With the help of the behavioral domain and paradigm class meta-data from the BrainMap database they characterized functional profiles of each of the eMDN regions and concluded that the eMDN is most likely the neurobiological substrate of EF. Through common activations Camilleri and colleagues proposed a core network of the eMDN consisting of the bilateral IFJ extending into the IFG, the bilateral aINS, and the bilateral pre-SMA extending into the anterior MCC.

Taking the neural basis into account, it becomes even more certain that EF are a macro-construct rather than a single process and they depend on distributed networks instead of any particular region, with a core network and more specific regions that can be activated depending on certain task demands (manuscript Camilleri et al., 2017; Müller et al., 2014; Wager & Smith, 2003).

Healthy Aging

Healthy aging is associated with altered behavioral performance and brain activation patterns on several cognitive tasks. Differences seem especially pronounced on difficult tasks that emphasize cognitive control processes (Drag, & Bieliauskas, 2010; Park et al., 2002), while on other tasks, like vocabulary measures (Park et al., 2002; Salthouse, 1996), implicit memory, and knowledge storage (Park et al., 2002), they seem relatively stable.

In the past 20 years, due to the development of neuroimaging, our knowledge about cognitive aging has greatly increased. Neuroimaging techniques, like structural and functional magnetic resonance imaging (fMRI) and positron emission tomography (PET), made it possible to investigate age-related structural and functional changes. Nevertheless, the underlying mechanisms remain poorly understood (Cabeza, Anderson, Locantore, & McIntosh, 2002; Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008). Findings indicate that the cognitive system is highly dynamic and adaptive (Greenwood, 2007; Park, & Reuter-Lorenz, 2009). Although the aging brain faces unfavorable changes, such as the decline of dopaminergic receptors, volumetric shrinkage of many structures, and reduced density of white matter, it also seems to seek a maintenance of homeostatic cognitive functions through functional reorganization (Park, & Reuter-Lorenz, 2009).

A common finding is the reduced lateralization of brain activation in older adults (Cabeza et al., 1997; Grady, McIntosh, Rajah, Beig, & Craik, 1999; Reuter-Lorenz et al., 2000), which is suggested to be due to compensatory functions as it is correlated with better performance in older adults (HAROLD [hemispheric asymmetry reduction in older adults]; Cabeza, 2002; Cherry, Adamson, Duclos, & Hellige, 2005; Fera et al., 2005; Gutchess et al., 2005; Reuter-Lorenz et al., 2001; Rypma, & D’Esposito, 2001). An activation shift from posterior to anterior regions (PASA; Davis et al., 2008) in the aging brain is also often reported. Cognitive operations are assumed to be less automatic in older adults, which may result in reduced activation of posterior brain regions and therefore greater demands for executive control processes, which leads to an increased modulation of the lateral PFC (Grady et al., 1994; Madden et al., 1997, 2002, 2010; Schulte et al., 2011). Reuter-Lorenz and Cappell (2008) postulated that the increased modulation of the lateral PFC compensates for less efficient neural circuits in older adults (CRUNCH [compensation-related utilization of neural circuits hypothesis]). In 2009 Park and Reuter-Lorenz united previous theories in the scaffolding theory of aging and cognition (STAC). They postulated that age-related structural and functional changes in the brain result in inefficient and/or noisy processing. Scaffolds describe a supportive framework, which helps to maintain behavioral performance at a relatively high level at age, through strengthening of existing connections, development of new connections, and disuse of connections that have become fragile or deficient. This leads to greater bilateral activation and hyperactivation of frontal areas in older adults. In 2002 Stern postulated two distinct mechanisms that underlie cerebral reorganization in aging: neural reserve and neural compensation. In neural reserve, older adults show an increased recruitment of a specific brain region or network, whilst in neural compensation, older adults recruit alternative networks, which compensate for the lost efficiency of a specific brain region or network. STAC and Stern's concept of neural compensation show strong similarities. Different to Stern's postulation though, STAC assumes that neural scaffolding is normal throughout the life-span. It is suggested to be even used by younger adults, when existing circuits can no longer meet the task requirements and the brain develops new pathways, for example in novel situations or when new learning is necessary (Park & Reuter-Lorenz, 2009). The finding that younger adults also engage in processing bilateral when task complexity increases (Banich, 1998; Park, & Reuter-Lorenz, 2009) is in line with these postulations. Whilst these theories assume different underlying mechanisms, they share the assumption of an age-related modulation of the lateral PFC.

Results from imaging studies regarding age-related changes in EF and its subcomponents working memory, inhibition, and attention are rather ambiguous. An often-reported age-related activation pattern is an increase in bilateral prefrontal activity (e.g. Emery, Heaven, Paxton, & Braver, 2008; Madden et al., 1999; Morcom, Good, Frackowiak,

& Rugg, 2003; Piefke, Onur, & Fink, 2012) and a decrease in occipital activity (e.g. Ansado, Monchi, Ennabil, Faure, & Joanette, 2012; Madden et al., 2002, 2010; Schulte et al., 2011). Other studies however report an occipital increase (e.g. Bloemendaal et al., 2016; Chmielewski, Yildiz, & Beste, 2014; Van Impe, Coxon, Goble, Wenderoth, & Swinnen, 2011; Zysset, Schroeter, Neumann, & von Cramon, 2007) and a frontal decrease in older adults (e.g. Bloemendaal et al., 2016; Lamar, Yousem, & Resnick, 2004; Paxton, Barch, Racine, & Braver, 2007b; Schulte et al., 2011). Moreover, the age-related reduction in hemispheric asymmetry is not consistently found (e.g. Carp, Gmeindl, & Reuter-Lorenz, 2010; Madden et al., 2002; Toepper et al., 2014). The amount of different, partly contradictory findings, illustrates the need for a quantitative data aggregation, in the form of a meta-analysis.

So far there are three meta-analyses investigating cognitive aging in EF. The first meta-analysis from Spreng, Wojtowicz, and Grady (2010) considered all available experiments probing EF in age, such as working memory, task switching, and inhibitory control. They found convergence of increased age-related activation in the bilateral DLPFC, the right MFG, the left SMA, and the left rostrolateral PFC. Younger adults had a greater convergence of activation in the right ventrolateral PFC compared to older adults. In 2012 Turner and Spreng conducted separate meta-analyses for the subcomponents working memory and inhibition and found different patterns of significant convergent activation. For working memory, both age groups showed significant convergence in regions of the lateral PFC in both hemispheres, but older adults showed an increase in convergence in anterior and younger adults in posterior regions of the DLPFC. Additionally, an age-related increased convergence was found in the bilateral SMA. Regarding inhibition, a “young-plus pattern” was found, implicating that both age groups recruited the same brain regions, but older adults showed an increased activation in these regions (bilateral IFG, SMA, DLPFC, and right aINS). The authors reasoned that cognitive aging is not associated with a general mechanism leading to a compensatory increase in PFC activity but more likely with a specific modification of the neural networks engaged in the processing of a certain task or task component. In 2014 Di, Rypma, and Biswal conducted activation likelihood estimation (ALE) and voxel based morphometry (VBM) meta-analyses. They found convergence of increased age-related activation in the bilateral DLPFC, the anterior cerebellum, and the left IFG. They further constructed conjunction analyses between functional and structural alteration maps and found overlap between functional hyperactivation and grey matter reduction in the DLPFC. Through further analyses they revealed that alterations in these regions were related to task performance, implicating that an increased activation in the DLPFC is linked to a better performance in older adults. All meta-analyses found convergence of activation in the lateral PFC, but differed regarding additionally activated regions as well as activation patterns of the subcomponents.

Current Study

The aim of the present study is to investigate regions affected by cognitive aging with regard to EF, whilst looking separately at their subcomponents working memory, inhibition, and attention. In line with recent meta-analyses (Di et al., 2014; Turner, & Spreng, 2012) the present study investigates working memory and inhibition, but will include experiments probing attention for the first time.

Coordinate-based ALE meta-analyses (Eickhoff et al., 2009; Eickhoff, Bzdok, Laird, Kurth, & Fox, 2012; Turkeltaub, Eden, Jones, & Zeffiro, 2002; Turkeltaub et al., 2012) are used to integrate results from neuroimaging studies investigating working memory, inhibition, and attention. The meta-analytic approach was chosen, because single studies have a reduced reliability as they rely on small sample sizes, which may lead to inaccurate findings (Button et al., 2013) and strongly depend on experimental and analytical procedures (Carp, 2012). Another shortcoming of single neuroimaging studies is the publication bias. Different to other scientific fields, the publication bias in neuroimaging is not equivalent to the file drawer problem, where studies in which the investigator fails to reject the null-hypothesis are thought to be less important and therefore not published (Rosenthal, 1979). The bias rather changes its direction, meaning that due to the high analytical flexibility (Carp, 2012) different approaches for data-analysis, inference and thresholding might be adjusted until a desired or significant result is found. Therefore, the publication bias in neuroimaging rather is a bias of less relevant and possibly random results (manuscript Müller et al., 2017). Meta-analyses have the advantage of more subjects and more variations in the tasks and analyses performed. Hence, they can overcome problems associated with individual neuroimaging studies and have more power to find the "true" activation through convergence across different neuroimaging experiments.

However, recent meta-analyses also show inconsistent findings. The divergence between the meta-analyses from Turner and Spreng (2012) and Di, Rypma, and Biswal (2014) is astonishing, since both used ALE to determine the convergence. Possible reasons for these differences are the inclusion of region of interest (ROI) studies in meta-analyses, the use of FDR-correction, and the low sample sizes (Müller et al., 2016, manuscript 2017). The current study aims to avoid these shortcomings in order to result in clusters of convergence that are closer to the "true" age-related changes in brain activation concerning EF and to discuss the findings with regard to previous meta-analyses and prominent aging theories.

Methods

Selection of Studies

Studies were searched in the databases Web of Science (http://apps.webofknowledge.com), PubMed (https://www.ncbi.nlm.nih.gov/pubmed/), PsycINFO (http://ovidsp.tx.ovid.com), and Google Scholar (http://scholar.google.de). They were selected using a systematic search approach, involving the following search strings: (1) title: "age" or "aging" or "ageing" or "age-related" or "older adults" or "old adults" or "adult life-span" or "elderly adults"; and (2) title: "executive functions" or "working memory" or "inhibition" or "attention"; and (3) abstract: "fMRI" or "functional magnetic resonance imaging" or "PET" or "positron emission tomography" or "neuroimaging" or "cerebral blood flow". When the first search approach was exhausted specific tasks related to each EF were included in the search string: (2) for working memory "n-back" or "sternberg" or "delayed match to sample" or "delayed simple matching" or "stimulus-response-compatibility"; for inhibition "stroop" or "flanker" or "simon" or "stop-signal" or "go/no-go"; and for attention "stimulus detection" or "stimulus discrimination" or "wisconsin card sorting" or "tower of london" or "task switching" or "dual task". The search criteria were partially motivated by previous meta-analyses regarding aging and EF (Di et al., 2014; Spreng et al., 2010; Turner, & Spreng, 2012). The decision on which tasks to include in the extended search string was made based on meta-analyses examining working memory (Rottschy et al., 2012), inhibition (Cieslik et al., 2014), and attention (Langner & Eickhoff, 2013). Furthermore, recent ALE studies (Di et al., 2014; Spreng et al., 2010; Turner, & Spreng, 2012), reviews, and reference lists of identified studies were searched for possible inclusion.

Inclusion and Exclusion Criteria

Only peer-reviewed fMRI or PET studies that contained healthy young and old subjects with absence of pharmacological manipulation, brain lesions, and mental or neurological disorders were included. Only studies covering the whole brain, with the rule of thumb that slice thickness times slices is greater than 80 millimeters, were included. This assumption is based on the measurements of a standard brain, which has a width of 140 mm (right-left), a length of 167 mm (posterior-anterior) and a height of 93 mm (inferior-superior not including the cerebellum; Carter, 2014). Furthermore, studies had to report whole brain group analyses as coordinates corresponding to a standard reference space, such as the Montreal Neurological Institute (MNI) or Talairach (Talairach, & Tournoux, 1988) space. Consequently, no ROI studies were included. However, it has to be mentioned that some of the included studies reported masking of the between-group contrast with the task-positive effect to only identify regions that were associated with the specific task. Only activation data resulting from subtraction between task and sensorimotor control or resting-baseline conditions or different levels of task difficulty were included. Thus, deactivation data, results from connectivity analyses, and those reporting correlations and interactions with other variables (e.g. group x performance interaction, correlation with reaction time) were not considered. If a study did not report the coordinates of activation maxima or other uncertainties occurred the authors were contacted. The studies, for which additional information to the published paper was gained, are marked in Table 1.

In the context of ALE the term “experiment” usually refers to any single (contrast) analysis on imaging data yielding localization information, while the term “study” usually refers to a scientific publication reporting one or more “experiments” (Eickhoff, and Bzdok, 2012; Laird et al., 2011). To minimize the risk that meta-analytic results are driven by within-group effects, the contribution of an experiment was limited to one experiment per study. Consequently, if a study reported more than one experiment that was suitable for inclusion, these findings were pooled into one experiment, as suggested from Turkeltaub and colleagues (2012), to prevent that multiple experiments from one study drive the convergence in some clusters. If a working memory study for example included separate experiments for encoding, maintenance, and retrieval, they were pooled into one experiment. If the study included experiments from easier and difficult conditions, the difficult conditions were chosen, because age-related changes are expected to be more prone in difficult tasks. Furthermore, when experiments of transient or sustained activity were available, experiments of transient activity were chosen as they allow to analyze more specific condition-related activation. Because the standard templates used in SPM (Statistical Parametric Mapping) - since version SPM96 (Müller et al., 2016) - and FSL (FMRIB Software Library) are in MNI space, coordinates of experiments using SPM or FSL were treated as MNI coordinates unless the authors explicitly reported a transformation from MNI to Talairach space or the use of an alternative brain template (see Table 2).

Based on these criteria - after screening the abstracts - 142 studies were retrieved. 87 of these were excluded later, because of ROI analyses, no between-group effects, no reported coordinates, unsuitable tasks, no imaging of the whole brain, unsuitable methods, unsuitable contrasts, or the use of the same subjects. This led to a total of 55 studies, 27 for working memory, 14 for inhibition, and 16 for attention. Please note that one study (Eich et al., 2016) was included for inhibition and attention and another one (Lamar et al., 2004) for inhibition and working memory, causing the deviance in the total number of studies. In cases were the affiliation to either of these categories were unclear, the study was assigned based on the author's characterization (Dorum et al., 2016) or the standard characterization of the task paradigm in the literature (Johnson, Mitchell, Raye, & Greene, 2004). Together these studies reported 781 activation foci obtained from 2,403 participants in 85 experiments.

Meta-analyses for EF – that is probing either working memory, inhibition, or attention - as well as meta-analyses for the subcomponents themselves were conducted. For EF and each subcomponent (1) pooled, (2) old > young, and (3) young > old meta-analyses were executed, which led to 12 meta-analyses. Pooled analyses search for aberrant activation, independent of the direction of the between-group effect. For neuroimaging findings pooled analyses may provide the best summary as the directions of group differences depend on how exactly group differences were calculated, which varies widely between experiments. Some may generate a task versus control contrast at the subject level, which is then compared between patients and controls and others may report group (old versus young) x task (task versus control or baseline) interactions at the second level. As a result, effects of between-group differences in activation for these control conditions may be influencing the overall direction of group differences unpredictably. This could possibly lead to an observed increase in activation when the task versus control contrast is generated at the subject level while group x condition interaction at second level would reveal decreased activation (Müller et al., 2016). The pooled meta-analysis for EF consisted of 55 experiments, the young > old meta-analysis of 41 experiments, and the old > young meta-analysis of 44 experiments. For the subcomponent working memory, the pooled meta-analysis comprised 28 experiments, the young > old meta-analysis 25 experiments, and the old > young meta-analysis 18 experiments. Regarding the subcomponent inhibition, the pooled meta-analysis consisted of 14 experiments, the young > old meta-analysis of 8 experiments, and the old > young meta-analysis of 13 experiments. Concerning the subcomponent attention, the pooled meta-analysis included 16 experiments, the young > old meta-analysis 9 experiments, and the old > young meta-analysis 15 experiments.

Furthermore, supplementary meta-analyses were conducted. To investigate if the performance has an effect on the activation, the meta-analyses young > old performance matched (16 experiments), young > old performance not matched (25 experiments), old > young performance matched (20 experiments) and old > young performance not matched (24 experiments) were executed. Previous studies found a correlation between enhanced performance in older subjects and additional contralateral activation (Cabeza et al., 2002; Fera et al., 2005; Reuter-Lorenz et al., 2001; Rypma & D'Esposito, 2001). In addition, working memory experiments were divided into experiments with manipulation and without manipulation. This is based on the notion that working memory is a rather heterogeneous concept (Rottschy et al., 2012). Some authors use the term working memory for holding information in mind for seconds to minutes (e.g. Podell et al., 2012; Toepper et al., 2014), while others would label this process as short-term memory and only consider the holding and active manipulation of information to be working memory (Baddeley, & Hitch, 1994; Smith, & Jonides, 1999). For this reason, further supplementary meta-analyses for working memory with manipulation pooled, working memory without manipulation pooled, working memory without manipulation young > old, and working memory without manipulation old > young were conducted. Since there were only 7 experiments for working memory with manipulation, only a pooled analysis was conducted. Working memory without manipulation yielded 21 experiments for the pooled analysis, 20 experiments for the contrast young > old and 15 experiments for the contrast old > young. Attention was also divided into task switching and selective attention to reduce the heterogeneity. Since there were only three experiments investigating selective attention, no meta-analysis on selective attention was conducted. Task switching was executed as a pooled meta-analysis, because there were merely 12 experiments to include. This led to 9 supplementary meta-analyses, and a total of 21 meta-analyses.

Based on a recent simulation study by Eickhoff and colleagues (2016) meta-analyses should include a minimum of 17 experiments. Otherwise they have low power and are prone to yield clusters of convergence that are almost exclusively driven by single experiments and thus the generalization of effects would be reduced. Some of the meta-analyses in the current study consist of less than 17 experiments, which is due to a limited amount of studies investigating age effects on attention and inhibition that meet the inclusion criteria. Those meta-analyses should be viewed as preliminary data and are thus interpreted with caution.

To conduct meta-analyses the data was transformed from Talairach into the MNI space as the two standard spaces used in neuroimaging differ from one another, with brains in

MNI being larger than those in Talairach space (Lancaster et al., 2007). Figure 1 portrays the steps conducted in the form of a flowchart.

Activation Likelihood Estimation

All meta-analyses were conducted using the revised version of the ALE algorithm for coordinate-based meta-analysis of neuroimaging results (Eickhoff et al., 2009, 2012; Turkeltaub et al., 2002, 2012) implemented as in-house MATLAB tools. This algorithm aims to identify areas showing a convergence of foci reported from different experiments, which is higher than expected under a random spatial association. ALE models the reported foci not as single points but as centers of 3D Gaussian probability distributions acknowledging the spatial uncertainty associated with each focus. The width of these uncertainty functions was determined based on empirical data on the between-subject (e.g. neuroanatomical variability and small sample sizes) and between-template variance (e.g. various brain templates, normalization and analysis strategies), which represent the main components of uncertainty in neuroimaging data. Essentially, the applied algorithm weights the between-subject variance by the number of examined subjects per study. Consequently, larger sample sizes should provide more reliable approximations of the "true" activation effect and should therefore be modelled by "narrower" Gaussian distributions (Eickhoff et al., 2009). The probability distributions of all activation foci of a given experiment were then combined for each voxel, which creates a modeled activation (MA) map (Turkeltaub et al., 2012). Taking the union across these MA maps yielded voxel-wise ALE scores describing the convergence of results at each particular location of the brain. ALE scores were compared to an empirical null distribution reflecting random spatial association among all MA maps to distinguish "true" convergence between studies from random convergence (e.g. noise). The resulting random-effect inference focuses on inference on the above-chance convergence across studies rather than clustering of foci within a particular study (Eickhoff et al., 2009). The null hypothesis was derived by computing the distribution that would be obtained when sampling a voxel at random from each of the MA maps and taking the union of these values in the same manner as for the (spatially contingent) voxels in the original analysis (Eickhoff et al., 2012). The *p* value of a "true" ALE score was then given by the proportion of equal or higher values obtained under the null distribution. The resulting non-parametric *p* values for each meta-analysis were cut off at a threshold of $p < .05$ (family-wise error corrected at cluster level; cluster inclusion threshold at voxel level: $p < .001$). For an illustration of the ALE approach see Figure 2. All resulting areas were anatomically labelled by reference to probabilistic cytoarchitectonic maps of the human brain using the SPM Anatomy Toolbox (Eickhoff et al., 2005, 2007).

Results

Executive Functions

In a first step a pooled meta-analysis across all experiments probing EF - that is belonging to the category of either working memory, inhibition, or attention and independent of the contrast direction - was conducted. This pooled meta-analysis revealed significant convergent activity in the left IFJ extending into the precentral gyrus (MNI = -44, +18, +28; -46, +6, +30; -32, +18, +28; see Table 3 and Figure 3A). Half of the contribution was driven by experiments investigating working memory (49.19%). The other half of the contribution was equally shared by experiments probing inhibition (25.52%), and attention (25.07%; see Table 4). In a next step, two meta-analyses were performed that looked for convergent activity depending on the direction of the contrast, e.g. young > old and old > young, respectively. The meta-analysis testing for convergent decreased activity across executive function experiments in older participants yielded a significant cluster of convergence in the right DLPFC (MNI = +40, +32, +20; +46, +32, +22; see Table 3 and Figure 3B). The cluster is almost equally shared by experiments probing working memory (51.44%), and inhibition

(48.56%; see Table 4). The meta-analysis testing for convergent increased activity across executive function experiments in older compared to younger subjects resulted in two clusters of significant convergence, in the left IFJ (MNI = -44, +14, +32), and the left primary and secondary visual cortex (V1; V2; MNI = -6, -66, +12; see Table 3 and Figure 3C). The convergence in the left IFJ was mostly driven by experiments that investigated inhibition, with 58.61%. Experiments testing attention contributed with 23.45% and experiments probing working memory with 17.92% (see Table 4). The convergent activity in V1 and V2 was almost equally driven by experiments that investigated working memory (34.18%), inhibition (31.88%), and attention (33.75%; see Table 4).

Additionally, four supplementary meta-analyses, taking the performance of the subjects into account, were conducted. The young > old meta-analysis for matched performance did not yield significant convergence, whereas the young > old meta-analysis for not matched performance resulted in significant convergence in the right DLPFC (MNI = +40, +32, +18; +48, +32, +22; see Table 3 and Figure 4), which was mostly driven by experiments that investigated working memory (62.81%) as well as inhibition (37.19%; see Table 4). The matched and not matched meta-analyses probing an increased convergent activity for older relative to younger subjects, did not reveal significant convergence.

Subcomponents

In a second step, meta-analyses for the subcomponents working memory, inhibition, and attention were conducted.

Working Memory. The pooled meta-analysis across working memory experiments revealed significant convergence in the left IFJ (MNI = -44, +18, +28; -40, +10, +24; -46, +10, +22; see Table 3 and Figure 5). The meta-analyses testing for convergent decreased and increased activity in older compared to younger subjects did not yield significant convergence.

Furthermore, four supplementary meta-analyses for working memory with manipulation and working memory without manipulation were conducted. The pooled meta-analysis probing experiments that investigated working memory with manipulation did not reveal significant convergence. For the pooled meta-analysis across working memory experiments without manipulation significant convergence was found in the lower part of the left precentral gyrus extending into area 44 (MNI = -40, +10, +22; -46, +8, +22; -50, +10, +32; see Table 3 and Figure 6). The meta-analyses testing for significant decreased or increased convergent activity in older compared to younger subjects probing working memory experiments without manipulation did not result in significant convergence.

Inhibition. The pooled meta-analysis across experiments probing inhibitory control yielded significant convergent activity in left visual areas (V1; V2; V3d; MNI = -16, -70, +12; -6, -66, +10; see Table 3 and Figure 7A). For the young > old meta-analysis significant convergence was found in the right DLPFC (MNI = +42, +40, +24; +36, +34, +24; see Table 3 and Figure 7B). The old > young meta-analysis resulted in significant convergence in left visual areas (V1; V2; V3d; MNI = -16, -70, +12; -6, -66, +10; see Table 3 and Figure 7C).

Attention. Four meta-analyses probing attention were conducted: a pooled meta-analysis, two directed meta-analyses, e.g. young > old and old > young, as well as a meta-analysis only probing experiments that investigated task switching. None of these meta-analyses yielded significant convergence of activation.

Discussion

Coordinate-based ALE meta-analyses were used to analyze the neural correlates of age-related changes in EF. Twelve main meta-analyses were executed. For EF – that is experiments probing either working memory, inhibition, or attention – and each subcomponent itself, pooled as well as directed meta-analyses, e.g. young > old and old > young, were conducted. Additionally, nine supplementary meta-analyses were executed, testing for an effect of performance and investigating working memory with and without manipulation as well as task switching separately.

The current study found convergence of activation mainly in three regions: the left IFJ, the right DLPFC, and left visual areas, primarily V1. Convergent increased activity in the left IFJ and V1 was found, while in the right DLPFC convergent decreased activity for older compared to younger adults was shown. The current findings are in line with CRUNCH (Reuter-Lorenz, & Capell, 2008), STAC (Park, & Reuter-Lorenz, 2009), and neural compensation (Stern, 2002). In the following paragraphs the results will be discussed separately for each region of convergence.

Left IFJ

Convergence in the left IFJ was found in the meta-analyses EF pooled, EF old > young, working memory pooled and working memory without manipulation pooled. The left IFJ is associated with spatial cognition, language, and memory (manuscript Camilleri et al., 2017). Its functional role may be to integrate information from these domains (Brass, Derrfuss, Forstmann, & von Cramon, 2005). Quantitative meta-analyses that investigated task switching, set shifting, and Stroop paradigms revealed significant convergence in the bilateral IFJ in the meta-analysis testing task switching and set shifting experiments and significant convergence in the left IFJ in the meta-analysis probing Stroop tasks (Derrfuss, Brass, Neumann, & von Cramon, 2005). To investigate the functional role of the IFJ Brass and von Cramon (2004) manipulated the number of times a task was prepared and demonstrated that the left IFJ was involved in task preparation. By manipulating the cue-task mapping they were able to show that this activation was related to updating of relevant task representations, a process that allows us to adjust our behavior to new environments. In another study Derrfuss, Brass, and von Cramon (2004) mapped the activity from experiments investigating working memory, task switching, and inhibitory control and found a significant overlap in the IFJ for all task types. Consequently, they suggested that the IFJ plays a more important role in cognitive control than previously thought. In line with these findings is the almost equal contribution of working memory (49,19%), inhibition (25,52%), and attention (25,07%) experiments to the IFJ cluster in the pooled EF meta-analysis, pointing out the importance of the left IFJ for all subcomponents, respectively.

A recent study (manuscript Camilleri et al., 2017) using task-dependent and task-independent functional connectivity analyses proposed the bilateral IFJ extending into the IFG together with the bilateral aINS, and the bilateral pre-SMA extending into the aMCC to form the core eMDN. The key role of the core eMDN may be to enable high levels of functional diversity and functional synchronization between regions (manuscript Camilleri et al., 2017) necessary for cognitive control. Taking these findings into account the left IFJ seems to be task, stimuli, and subcomponent independent.

An explanation for the convergent increase of activity in older compared to younger adults may be that the updating of task representations and the integration of spatial cognition, language, and memory might require more effort for older adults, which leads to a greater need of recruiting the left IFJ. This age-related over-recruitment of the lateral PFC is in line with several neuroimaging studies (e.g. Cabeza et al., 2002; Emery et al., 2008; Morcom et al., 2003) as well as cognitive aging theories proposing an age-related modulation in the lateral PFC (Cabeza, 2002; Davis, 2008; Park, & Reuter-Lorenz, 2009; Reuter-Lorenz, & Cappell, 2008). However, to make further conclusions regarding this over-recruitment, the findings need to be linked to performance. The current study did investigate effects of performance in supplementary meta-analysis, but these did not reveal significant convergence.

Right DLPFC

Convergence in the right DLPFC was found in the EF young > old, EF young > old performance not matched, and inhibition young > old meta-analyses. The right DLPFC is important for goal-maintenance (Paxton et al., 2007). A decreased convergent activity in older compared to younger subjects in the right DLPFC might seem unexpected at first glance, since most cognitive aging theories and the majority of studies investigating EF report an age-related increase in DLPFC activity (e.g. Emery et al., 2008; Milham et al., 2002; Piefke et al., 2012). However, when taking the specific task demands into account, some studies report an age-related increase in right DLPFC activity during simple task conditions, such as short delay or low memory load, but an age-related decrease in right DLPFC in more complex conditions (Cappell, Gmeindl, & Reuter-Lorenz, 2010; Carp et al., 2010; Mattay et al., 2006; Schneider-Garces et al., 2009). These findings are in line with the dedifferentiation hypothesis of cognitive aging (Goh, 2011) which suggests that brain regions showing specialized responses to specific cognitive tasks become less specialized with increasing age. The brain thus responds in a rather general manner to all tasks with decreased activation in task-relevant regions and increased activation in less specialized regions. The current study included the difficult task condition, when difficult and less difficult task conditions were available, because age-related changes were expected to be more prone in difficult tasks. The inclusion of difficult task conditions could thus explain the resulting pattern of increased convergence within the right DLPFC for younger compared to older adults.

The DLPFC is commonly assumed to play a crucial role in executive control. But it seems that the role of the IFJ might be just as important. According to Brass and colleagues (2005) the primary role attributed to the DLPFC in the context of cognitive control is owed to the fact that consistent activation in the IFJ has been ignored.

Left Visual Areas

Convergence in left visual areas, primarily in V1, was found in the EF old > young, inhibition pooled, and inhibition old > young meta-analyses. V1 was for a long time thought of as less specialized, more basal region, responsible for visual processing (e.g. Luck, & Ford, 1998). However, there are uncertainties if V1 is only responsible for passive image-processing. It was suggested that there is a bidirectional progression of attentional effects in the ventral stream, implicating that V1 modulates higher-level visual areas through feedback (Buffalo, Fries, Landman, & Liang, 2010). Consequently, visual perception may be a highly integrative process that incorporates not only inputs from V1 but also V1 cortical circuitry directly (Somers, Dale, Seiffert, & Tootell, 1999). Taken the reduced age-related convergence in the right DLPFC into account, this would support the idea of older adults recruiting altering neural networks to maintain a normal level of task performance (Reuter-Lorenz, & Cappell, 2008). Activation in the right DLPFC has previously been linked to task performance, in terms of a positive correlation between performance and activity in this region (Bloemendaal et al., 2016; Paxton et al., 2007a; Schulte et al., 2011). The age-related decrease in right DLPFC might thus reflect an age-related deficit in goal-maintenance, which is also important for the encoding of cue information, and results in an increased recruitment of primary visual areas to compensate for these impairments. Furthermore, it was suggested that the age-related decrease in frontal and increase in visual activation reflects impaired response selection (Schulte et al., 2011), which is also part of inhibitory control when subjects have to select the response alternative of withholding or suppressing an already initiated motor response. Tasks may thus become more repetitive and older adults might therefore use less executive attentional control systems and more visual areas (Schulte et al., 2011). Besides, age-related declines in cognitive control could make older adults more susceptible to the influence of automatic, bottom-up processes (Braver, & Barch, 2002; Park,

& Reuter-Lorenz, 2009), suggesting that the inhibition of automatic responses is impaired in older adults.

Comparison to Previous Meta-Analyses

The current results deviate quite noticeably from previous meta-analyses. Turner and Spreng (2012) revealed convergence for both age groups in regions of the lateral PFC in both hemispheres, whereas older adults showed an increase in convergence in anterior regions and younger adults in posterior regions of the DLPFC. Additionally, they found increased age-related convergence in the bilateral SMA. For inhibition, they found a “young-plus” pattern. Older adults showed convergence in the same brain regions as younger adults, but to a greater extent (bilateral IFG, SMA, DLPFC, and right aINS). The current study revealed increased age-related convergence in the left V1 and decreased convergence in the right DLPFC. On the basis of their different findings for working memory and inhibition, Turner and Spreng see their results as support for a process-specific account of EF and cognitive aging. While the current findings also show different activation patterns, a conclusion can only be made by directly contrasting the subcomponents against each other, which was not possible in the current study due to an insufficient number of experiments for the subcomponents inhibition and attention. Di and colleagues (2014) found convergent age-related increased activity in the bilateral DLPFC, the anterior cerebellum, and left IFG for executive function experiments, but did not find differences in DLPFC hyperactivation between working memory and inhibition.

The following shortcomings of the previous meta-analyses might explain the differences in results. First, the previous meta-analyses included ROI analyses or papers of ROI analyses and did not specify whether they received additional material from the authors that was not published. Given that the null distribution in ALE reflects a random spatial association between findings across the entire brain under the assumption that each voxel a priori has the same chance of being activated (Eickhoff et al., 2012), inclusion of ROI analyses would violate this assumption, and lead to inflated significance for those regions that come from ROI analyses (manuscript Müller et al., 2017). Therefore, all included coordinates must be derived from whole-brain analyses. Second, the previous meta-analyses attempted to correct for multiple comparison by controlling the voxel-level false discovery rate (FDR), which is invalid for topographic inference on smooth data (Chumbley, and Friston, 2009). This is supported by a previous simulation study for ALE, which demonstrated that voxel-wise FDR correction features low sensitivity and leads to inflated positive findings (Eickhoff et al., 2016). Instead, Eickhoff and colleagues recommend the use of cluster-level FWE correction for ALE meta-analyses because it provides good sensitivity and low susceptibility to false positives. Third, the previous meta-analyses consisted of small sample sizes. Meta-analyses should consist at least of 17 experiments. They otherwise have low power and are prone to yield clusters of convergence that are almost exclusively driven by single experiments (Eickhoff et al., 2016). Although inclusion of more experiments provides higher power for smaller effects it also often compromises the homogeneity of the included experiments (manuscript Müller et al., 2017). The current study aimed to achieve a balance between homogeneity and robustness by setting strict inclusion and exclusion criteria. This might have led to different results compared to previous meta-analyses (Di et al., 2014; Turner & Spreng, 2012). Turner and Spreng as well as Di and colleagues included ROI experiments and tasks that could not be linked to inhibition (Mell et al., 2009; included by Turner, & Spreng, 2012, & Di et al., 2014) or depended on another variable, such as reaction time (Tam, Luedke, Walsh, Fernandez-Ruiz, & Garcia, 2015; included by Turner & Spreng, 2012).

A huge problem is that a detailed description of the included contrasts in the previous meta-analyses were missing as well as information on whether additional information for the studies included was derived, thus making a replication very difficult and compromising comparability. The combination of low sample sizes and FDR thresholding may have rendered previous meta-analyses very liberal, leading to high convergence across the literature (Müller et al., 2016).

Another issue is the labeling of the DLPFC. When comparing the coordinates revealed by Turner and Spreng (2012) labeled as left DLPFC with the cluster of the present pooled EF analysis yielding convergence in the left IFJ in MRIcron (Chris Rorden; http://people.cas.sc.edu/rorden/mricron/index.html) their DLPFC coordinate was lying in the present IFJ cluster. The current study found the same for coordinates labeled as left DLFC from Di and colleagues (2014). On the one hand this suggests that the current results do match the one's from previous meta-analyses at least to a certain extent. On the other hand, however, this raises the issue of unclear labeling, which again affects conclusions about the functional role of certain brain regions and their role in cognitive aging as well as the qualitative comparability of studies.

Non-Significant Findings

No significant convergence was found for the following meta-analyses: EF performance matched young > old, EF performance matched old > young, EF performance not matched old > young, working memory without manipulation pooled, attention pooled, attention young > old, attention old > young, and task switching pooled. Causes for these non-significant findings might be the analytical flexibility, e.g. analysis software, preprocessing parameters, specific contrast calculated (interactions or main effects) which adds heterogeneity to the literature (Müller et al., 2016). Of the included studies, 37 performed statistical inference without correction for multiple comparisons (see Table 1). Uncorrected inference is more sensitive to meaningful (small) effects but also contaminates the literature with false-positive findings (Bennett, Wolford, & Miller, 2009). False-positive findings based on invalid inference are more likely to be published than null findings using valid inference (Gold, Powell, Xuan, Jicha, & Smith, 2010). Unlike effect-size meta-analyses, coordinate-based meta-analyses are not affected by non-published effects or published false-positive effects, since they assess spatial convergence between reported activation coordinates rather than quantifying the pooled effect size as in effect-size meta-analyses. Consequently, the null hypothesis to reject is not the absence of any effect but rather that spatial convergence among published coordinates is random. Although ALE meta-analyses are less susceptible to publication bias, they should not be considered an absolute truth but rather as a quantitative integration of the published knowledge and a statistical synopsis of the current state of the field (Rottschy et al., 2012).

Furthermore, the lack of significant findings in some meta-analyses suggests the existence of process-specific differences in the patterns of age-related functional brain change, even within the relatively narrow context of working memory and attention (Rajah, & D'Esposito, 2008). In a previous meta-analysis probing working memory experiments Rottschy and colleagues (2012) found convergence in different brain regions for different demands. Load-effects for example resulted in convergence in a bilateral inferior frontal network, while task-set effects, e.g. concentration on task-relevant information to maintain task goals, were more prominent in the left hemisphere including rostral lateral PFC and superior parietal lobule (SPL)/IPS as well as aINS. Furthermore, verbal working memory tasks revealed greater convergence in left Broca's region, while non-verbal tasks resulted in convergence in dorsal and medial premotor areas. Since the current study included verbal and non-verbal working memory tasks as well as tasks investigating load effects and simple goal maintenance tasks, an additional division seems appropriate, to allow further insights of age-related changes in working memory. A similar distinction can be observed for attentional control. A meta-analysis probing vigilant attention (Langner, & Eickhoff, 2013) yielded convergence in dorsomedial, mid- and ventrolateral PFC, anterior insula, parietal regions (intraparietal sulcus, temporoparietal junction), and subcortical structures (cerebellar vermis, thalamus, putamen, midbrain), while a meta-analysis investigating task switching revealed convergence in the bilateral IFJ, superior frontal gyrus (DFG), left IFG, ACC, right IFS, anterior cingulate cortex [ACC]/pre-SMA, and insula (Derrfuss et al., 2005). Taking these findings into account, a further subdivision of working memory and attentional control seems important to investigate whether the current null findings are partly due to a process-specific account of these subcomponents.

There are some technical considerations that need to be acknowledged. Although ALE is a well-validated and widely used coordinate-based meta-analytic approach, it stands to reason that an image-based meta-analysis may have provided greater sensitivity as it would provide the full information of the original study in the image (Salimi-Khorshidi, Smith, Keltner, Wager, & Nichols, 2009). However, as imaging data is rarely shared, a sufficient number of experiments with whole-brain images of effect estimates and standard errors would have been considerably more difficult or even impossible to find. Additionally, some of the current meta-analyses included less than 17 experiments, because not enough studies that fit the inclusion criteria were available. The current findings for inhibition and null-findings for attention should therefore be viewed as preliminary data, since they have low power and the generalization of the found convergence is reduced (Eickhoff et al., 2016). Lastly, pooled meta-analyses might provide the most stable findings because directions of group differences depend on how exactly group differences were calculated and might unpredictably influence the overall direction of group differences. However, by reviewing the cluster contributions and original studies the current findings for directed group differences do not seem to be altered.

Conclusion

The current study revealed three regions affected by cognitive aging: the left IFJ, the right DLPFC, and the left V1. The findings support the proposal of Camilleri and colleagues (manuscript, 2017) that the IFJ is a core region of EF, which is activated across tasks, stimuli, and subcomponents. The updating of task representations and the integration of spatial cognition, language, and memory may require more effort for older adults, which might result in an increased need to recruit the left IFJ. Age-related convergent decreased activity in the right DLPFC and age-related convergence of increased activity in the left V1 may represent an impairment of goal-maintenance in older adults, which results in difficulties to encode and maintain cue information, and in turn the need to recruit different neural circuits. Linking the results to existing theories of age-related changes, the results support the use of neural scaffolds in terms of greater activation and additional neural circuits in the aging brain (Park, & Reuter-Lorenz, 2009; Reuter-Lorenz, & Cappell, 2008; Stern, 2002). Furthermore, the current findings did not reveal a posterior to anterior shift in aging (Davis et al., 2008) and an age-related hemispheric asymmetry reduction (Cabeza, 2002).

Finally, the current results indicate variations across individual experiments investigating age-related changes in EF and point out problems related to the replication of neuroimaging meta-analyses. While the deviant findings of previous meta-analyses could be due to conceptual and technical factors, a definite conclusion cannot be drawn without a proper replication. The latter is difficult to conduct, due to a lack of specific information, e.g. the specific contrasts included, or whether more material was obtained by the author of the original study.

Future Research

For future meta-analyses it is important to transparently report the choices made and provide a detailed description of inclusion and exclusion criteria and their motivation, precise reporting of the included papers and contrasts, as well as information on whether further information was received from the author of the original study (for guidelines see manuscript Müller et al., 2017). Another lack is the diversity of topographic labels, especially when it comes to the DLPFC. A precise description of the localization would be more adequate than a broad labeling, particularly of a not well-defined region such as the DLPFC.

It would be interesting for future research to take education into account. It was shown that highly educated individuals tend to be involved in more stimulating activities and thus are suggested to be more resilient to cognitive decline (Bennett et al., 2003; Wilson, & Bennett, 2003). Consequently, a further division into individuals with high and low education levels seems adequate.

The current study revealed age-related changes with regard to difficult task conditions. It was hypothesized that the age-related convergent decrease in frontal areas and increase in posterior areas could be a result of high task demands. To further investigate this proposition, future research could replicate the current study, but choose less difficult task conditions, to investigate whether the level of task demand has an impact on age-related changes in activation patterns.

In general, more single studies are necessary, to appropriately investigate inhibition and attention. Up to now, less than 17 experiments for the subcomponents inhibition and attention were available. The current findings concerning inhibition and attention should thus be viewed as preliminary data and can only be interpreted with caution. The future inclusion of more studies would not just allow for more powerful meta-analyses, but would also make a further subdivision of the subcomponents possible. Especially for attention a division into task switching and selective attention seems interesting to investigate. With more studies, it would also be possible to test the process-specific account of EF by directly contrasting the subcomponents with each other.

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Table 1

Overview of All Studies Included Comprising Information About the Mean Age and Number of Activation Foci for Each Age Group, the Performance, and Correction

Study #	First author	Year	n	Age Young[a]	Foci	Age Old[a]	Foci	Performance	Correction
Working Memory									
1	Angel	2016	20	25.4 (2.98)	3	66.8 (4.85)	4	=	uncorrected
2	Anguera	2010	18	21.1 (2.5)	1	71.4 (4.2)	10	≠	uncorrected
3	Bäckman	2011	20	25.2 (22-30)	2	70.3 (65-75)	-	≠	uncorrected
4	Bennett	2013	20	21.8 (2.5)	1	65.3 (5.3)	3	≠	corrected
5	Cabeza	1997	12	25.7 (19-31)	3	70.5 (67-75)	3	=	corrected
6	Carp	2010	18	20.9 (1.63)	10	68.3 (6.67)	-	≠	uncorrected
7	Emery[b]	2008	10	21.9 (2.6)	-	71.2 (6.2)	37	=	corrected
8	Fakhri	2012	16	21 (3.7)	5	68 (7.9)	5	=	corrected
9	Freo	2005	13	27 (6)	2	65 (11)	3	=	uncorrected
10	Grady	1998	13	25 (3)	12	66 (4)	3	≠	uncorrected
11	Grady	2007	16	26.1 (3.7)	-	65.8 (4.5)	8	≠	uncorrected
12	Gutchess	2005	13	21 (2)	9	70 (3.44)	15	≠	uncorrected
13	Haut	2005	6	23.3 (1.6)	1	67.3 (10.4)	-	≠	uncorrected
14	Johnson	2004	7	19.6	1	65.3	-	≠	uncorrected
15	Kurth	2016	20	23.4 (8.7)	2	74.4 (5.6)	10	=	corrected
16	Lamar	2004	16	27.9 (5.6)	13	69.1 (5.6)	4	≠	uncorrected
17	Madden	1999	12	23.17 (2.86)	2	71.0 (4.67)	9	≠	uncorrected
18	Meier	2014	21	24.6 (0.69)	4	57.8 (1.49)	-	≠	corrected
19	Morcom	2003	14	21 (1.6)	1	68 (3.3)	6	=	uncorrected
20	Nyberg	2009	11	23.64 (2.91)	3	68.82 (1.47)	1	≠	uncorrected
21	Park	2010	19	22.2 (2.4)	4	64.8 (2.8)	0	=	uncorrected
22	Paxton[b]	2007a	20	22.8 (3.7)	36	73 (5.7)	60	=	uncorrected

23	Podell	2012	11	< 35	16	> 65	-	≠	corrected
24	Prakash	2012	25	23.4 (3.3)	4	72.16 (4.6)	-	≠	uncorrected
25	Raye	2008	14	23	4	68	5	≠	uncorrected
26	Ricciardi	2009	10	26.2 (1.4)	7	68.4 (4.0)	13	=	uncorrected
27	Toepper	2014	18	26.8 (6.7)	5	71.7 (5.4)	-	≠	corrected
Inhibition									
1	Bloemendaal	2016	23	22.7 (0.6)	15	67.6 (0.7)	19	≠	uncorrected
2	Eich	2016	62	25.82	-	64.84	6	≠	uncorrected
3	Huang	2012	15	25.53 (3.48)	-	66.07 (4.15)	23	≠	uncorrected
4	Korsch	2014	19	22.95 (2.72)	-	70.26 (3.49)	1	≠	uncorrected
5	Lamar	2004	16	27.9 (5.6)	6	69.1 (5.6)	8	≠	uncorrected
6	Langenecker	2003	13	26.3 (5.5)	9	71.1 (5.4)	26	≠	uncorrected
7	Lee	2006	9	29.8 (6.2)	-	65.2 (4.2)	3	≠	uncorrected
8	Madden	2002	12	23 (2.13)	5	66.5 (4.96)	-	≠	corrected
9	Milham	2002	10	23	6	68	4	≠	uncorrected
10	Onur	2011	13	24.23 (3.09)	4	63.81 (6)	1	≠	uncorrected
11	Paxton[b]	2007b	16	21.56 (3.14)	1	72.38 (6.51)	29	≠	uncorrected
12	Persson[b]	2007	28	21.7 (2.5)	-	68.1 (5.8)	4	≠	corrected
13	Schulte	2011	14	23.6	9	71	16	≠	uncorrected
14	Zysset	2007	23	26.6 (3.6)	-	57.1 (6.49)	10	=	uncorrected
Attention									
1	Ansado	2012	16	23.31 (3.42)	4	67.82 (3.21)	9	≠	corrected
2	Chmielewski	2014	14	60.51 (3.34)	-	24.37 (2.89)	2	≠	uncorrected
3	Davis	2008	14	22.2 (2.5)	3	69.2 (7.6)	2	=	uncorrected
4	Dorum	2016	21	24.42 (5.06)	6	64.67 (7.44)	-	≠	corrected
5	Eich	2016	62	25.82	7	64.84	21	≠	uncorrected
6	Fernandes	2006	12	26.33 (3.36)	4	71.18 (4.07)	18	≠	uncorrected
7	Grady	2010	10	25 (3)	10	66 (4)	18	≠	uncorrected
8	Kunimi	2016	20	23.85 (5.43)	-	67.35 (4.27)	22	≠	corrected
9	Kuptsova	2016	69	20-30	-	51-65	29	≠	corrected

10	Madden	1997	12	24.33 (2.01)	5	65.5 (5.2)	5	=	corrected
11	Madden	2010	20	22.4 (2.5)	1	69.6 (6.05)	17	≠	uncorrected
12	O'Connell	2012	14	22 (3.3)	-	70.6 (4.2)	2	≠	corrected
13	Steffener[b]	2016	63	25.79 (2.7)	-	65.47 (2.89)	13	≠	corrected
14	Townsend	2006	10	27.9 (18-41)	3	70.7 (65-89)	24	=	corrected
15	Van Impe	2011	20	25.2 (3)	7	68 (4.19)	-	≠	corrected
16	Zhu	2015	28	32 (3.8)	-	68.4 (5.4)	18	≠	corrected

Note. # = number, n = number of subjects for the smaller group, which is used in ALE to model the Gaussian kernel. = matched, ≠ non-matched. [a]age in mean and standard deviation as retrieved from the original study. [b]further material was derived from the author of the original study.

Table 2

Further Details Regarding Task, Contrast, Masking, Standard Reference Space, and Imaging Technique of All Studies Included

Study #	First author	Year	Task	Contrast	Specific contrast	Masked	Space	Imaging
Working Memory								
1	Angel	2016	Recognition Memory	Hits > CR	old > new	masked	MNI	fMRI
2	Anguera	2010	Spatial WM	WM manipulation > WM	WM > WM control	masked	MNI	fMRI
3	Bäckman	2011	Spatial Delayed Matching	WM high load > WM low load	load 6 > load 4	unmasked	MNI[a]	fMRI
4	Bennett	2013	Delayed Item Recognition	WM > baseline WM high load > WM low load	maintenance > rest load 6 > load 2 (retrieval)	masked	MNI	fMRI
5	Cabeza	1997	Word Recognition	WM difficult > WM medium	recall > recognition (LV2, LV4)	unmasked	TAL	PET
6	Carp	2010	Delayed Item Recognition	WM high load > WM low load	7 letters > 4 letters / 3 filled circles > 1 filled circle (encoding, maintenance)	unmasked	MNI	fMRI
7	Emery	2008	Letter-Number Sequencing	WM manipulation > WM	manipulation > maintenance	unmasked	TAL	fMRI
8	Fakhri	2012	Probe Recognition	WM > baseline	visual probe recognition > rest verbal probe recognition > rest auditory probe recognition > rest	unmasked	MNI	fMRI

9	Freo	2005	Delayed Match-to-sample	WM > baseline	face recognition > rest	unmasked	TAL	PET
10	Grady	1998	Delayed Match-to-sample	WM > control WM difficult > WM easy	averaged match-to-sample > averaged sensorimotor control 6s delay > 1s delay	unmasked	TAL	PET
11	Grady	2007	N-back	WM manipulation > baseline	sound category > rest	unmasked	TAL	fMRI
12	Gutchess	2005	Picture Encoding	Hits > Misses	remembered > forgotten	unmasked	MNI	fMRI
13	Haut	2005	Number-Letter Sequencing	WM manipulation > WM	number-letter sequencing > number-letter span	unmasked	MNI[a]	PET
14	Johnson	2004	Word Refreshing	WM > control	refresh > read (fast hits)	unmasked	TAL	fMRI
15	Kurth	2016	Probe Recognition	WM high load > WM low load WM high load > control	load 5 > load 2 load 5 > active baseline	unmasked	MNI	fMRI
16	Lamar	2004	Delayed Match-to-sample	WM > control	DMTS > perceptual control	unmasked	TAL	fMRI
17	Madden	1999	Recognition Memory	WM > control	encoding > control retrieval > control	unmasked	TAL	PET
18	Meier	2014	Item Recognition	WM difficult > WM easy	bound > unbound (encoding, maintenance)	unmasked	MNI	fMRI
19	Morcom	2003	Successful Memory Encoding	Hits > Misses	remembered > forgotten	masked	MNI[a]	fMRI
20	Nyberg	2009	N-back	WM > baseline WM high manipulation > WM low manipulation	1-back > rest 3-back > 2-back	unmasked	MNI	fMRI

21	Park	2010	Spatial Judgment	WM manipulation > control	coordinate task > response matched control task	unmasked	MNI	fMRI
22	Paxton	2007a	AX-CPT	WM difficult > WM easy WM > baseline	long delay > short delay task > rest	unmasked	TAL	fMRI
23	Podell	2012	Updating WM	WM difficult > WM easy	updating > overwriting	masked	MNI	fMRI
24	Prakash	2012	N-back	WM manipulation > WM	2-back > 1-back	masked	MNI	fMRI
25	Raye	2008	Refreshing	WM > control	refresh > read	unmasked	TAL	fMRI
26	Ricciardi	2009	Delayed Match-to-sample	WM > control	delay > sensorimotor control	masked	TAL	PET
27	Toepper	2014	Spatial WM Retrieval	WM > control	retrieval > active baseline	unmasked	MNI	fMRI
Inhibition								
1	Bloemendaal	2016	Load Dependent Stop-signal Anticipation	Hits > False Alarm Hits > Misses	high proactive response slowing > low proactive response slowing (level V, C) StopSuccess > StopFailure StopSuccess > Go	unmasked	MNI	fMRI
2	Eich	2016	Stimulus response incongruity	inhibition > automatic response	incongruent trials > congruent trials single incongruent > single congruent	unmasked	MNI	fMRI
3	Huang	2012	Stroop like	inhibition > automatic response	incongruent > congruent	unmasked	MNI	fMRI

4	Korsch	2014	Mixed Flanker-Stimulus-Response-Conflict	inhibition > automatic response	both incongruent > both congruent	masked	MNI	fMRI
5	Lamar	2004	Delayed Non-match to Sample	inhibition > control	DNMTS > perceptual control	unmasked	TAL	fMRI
6	Langenecker	2003	Stroop	inhibition > automatic response	incongruent > congruent incongruent > neutral	unmasked	TAL	fMRI
7	Lee	2006	Response Regulation	inhibition > automatic response	incompatible > compatible	unmasked	MNI	fMRI
8	Madden	2002	Visual Search	inhibition difficult > inhibition easy inhibition difficult > inhibition medium	conjunction > feature conjunction > guided	masked	TAL	PET
9	Milham	2002	Stroop	inhibition > automatic response	incongruent > congruent/neutral	unmasked	TAL	fMRI
10	Onur	2011	Stroop/Simon like	inhibition > automatic response	incongruent > congruent	unmasked	MNI	fMRI
11	Paxton	2007b	AC-CPT	inhibition > baseline	"BX" probes > rest	unmasked	TAL	fMRI
12	Persson	2007	Verb Generation	inhibition > baseline	many > rest	masked	MNI[a]	fMRI
13	Schulte	2011	Stroop Match-to-sample	inhibition > automatic response	incongruent > congruent (mixed and same response blocks, cue-target match or non-match trials)	unmasked	MNI	fMRI
14	Zysset	2007	Stroop	inhibition > automatic response	incongruent > neutral	unmasked	TAL	fMRI
Attention								
1	Ansado	2012	Letter-name matching	selective attention > control high capacity > low capacity	high capacity > reference task capacity 5 > capacity 3	unmasked	MNI	fMRI

2	Chmielewski	2014	Dual Task	task switching > baseline	PRP > noise	unmasked	TAL	fMRI
3	Davis	2008	Episodic Retrieval/Visual Perception	selective attention > baseline	overall task activity > rest	masked	MNI	fMRI
4	Dorum	2016	Multiple Object Tracking	task switching > single task	2 items > 1 item	unmasked	MNI[a]	fMRI
5	Eich	2016	Task Switching	task switching > single task	dual decisions > single decisions	unmasked	MNI	fMRI
6	Fernandes	2006	Divided Attention	divided attention > full attention	recognition divided > recognition full	unmasked	TAL	fMRI
7	Grady	2010	Face Discrimination	stimulus discrimination > control	face > noise image	unmasked	TAL	PET
8	Kunimi	2016	Task Switching	task switching > baseline	task high speed > rest task medium speed > rest	unmasked	TAL	fMRI
9	Kuptsova	2016	Task Switching	task switching > single task	dual decisions > single decisions	unmasked	MNI	fMRI
10	Madden	1997	Visual Search	divided attention > baseline divided attention > control	divided > passive divided > central	unmasked	TAL	PET
11	Madden	2010	Task Switching	task switching > baseline	on task period > ITI	masked	TAL	fMRI
12	O'Connell	2012	Oddball	stimulus discrimination > baseline	distractor > rest target > rest	unmasked	MNI[a]	fMRI
13	Steffener	2016	Task Switching	task switching > baseline	task switching > rest	masked	MNI	fMRI
14	Townsend	2006	Attention Shifting/Sustained Attention	task switching > baseline sustained attention > baseline	shift > rest focus > rest	masked	TAL	fMRI

15	Van Impe	2011	Dual Task	task switching > baseline	dual > rest	unmasked	MNI	fMRI
16	Zhu	2015	Task Switching	task switching > baseline task switching > single task	switch > rest switch > nonswitch	unmasked	MNI	fMRI

Note. # = number, WM = working memory. CR = correct rejection, PRP = psychological refractory period, ITI = inter trial interval.
[a]treated as MNI coordinates, because the original experiment used SPM/FSL.

Table 3

Brain Regions Showing Significant Convergence of Activity in Executive Functions and Their Subcomponents

Cluster/Macroanatomical Structure	Cytoarchitectonic Location (overlap in %)[a]	Cluster Size (voxel)	MNI Coordinates			Z_{max}
			x	y	z	
Executive Functions						
Pooled						
L IFG pars triangularis	L area 44 (17.3) L area 45 (4.2)	433	-44	+18	+28	5.22
L precentral gyrus	L area 44 (17.3) L area 45 (4.2)	433	-46	+6	+30	3.87
-	L area 44 (17.3) L area 45 (4.2)	433	-32	+18	+28	3.25
young > old						
R middle frontal gyrus	R area 45 (5.4)	147	+40	+32	+20	4.47
R middle frontal gyrus	R area 45 (5.4)	147	+46	+32	+22	3.93
old > young						
L IFG pars opercularis	L area 44 (3.7) L area 45 (2.3)	149	-44	+14	+32	4.13
L calcarine gyrus	L area hOc1 (V1; 39.9) L area hOc2 (V2; 23.2)	110	-6	-66	+12	4.72
Performance						
young > old not matched						
R middle frontal gyrus	R area 45 (8.4)	136	+40	+32	+18	4.56
R middle frontal gyrus	R area 45 (8.4)	136	+48	+32	+22	4.04
Working memory						
Pooled						
L IFG pars triangularis	L area 44 (12.8)	146	-44	+18	+28	3.83
L IFG pars triangularis	L area 44 (12.8)	146	-40	+10	+24	3.81
L IFG pars opercularis	L area 44 (12.8)	146	-46	+10	+22	3.61

Without manipulation						
Pooled						
L IFG pars opercularis	L area 44 (35.8)	153	-40	+10	+22	4.00
L IFG pars opercularis	L area 44 (35.8)	153	-46	+8	+22	3.82
L precentral gyrus	L area 44 (35.8)	153	-50	+10	+32	3.49
Inhibition						
Pooled						
L calcarine gyrus	L area hOc1 (V1; 35)	140	-16	-70	+12	4.47
	L area hOc2 (V2; 26.9)					
	L area hOc3d (V3d; 2.4)					
L calcarine gyrus	L area hOc1 (V1; 35)	140	-6	-66	+10	4.04
	L area hOc2 (V2; 26.9)					
	L area hOc3d (V3d; 2.4)					
young > old						
R middle frontal gyrus		102	+42	+40	+24	4.18
R middle frontal gyrus		102	+36	+34	+24	4.04
old > young						
L calcarine gyrus	L area hOc1 (V1; 35.7)	176	-16	-70	+12	4.67
	L area hOc2 (V2; 23.9)					
	L area hOc3d (V3d; 1.7)					
L calcarine gyrus	L area hOc1 (V1; 35.7)	176	-6	-66	+10	4.25
	L area hOc2 (V2; 23.9)					
	L area hOc3d (V3d; 1.7)					

Note. L = left hemisphere, R = right hemisphere. Z_{max} = maximum z-score of the local maxima, IFG = inferior frontal gyrus.
[a]cytoarchitectonic locations of the cluster's mean.

Table 4

Single Studies Contributing to the Clusters of Convergence

Analysis	Studies	Contribution in %
Executive Functions		
Pooled	Bäckman 2011	2.7
	Bloemendaal 2016	6.48
	Carp 2010	5.24
	Chmielewski 2014	0.92
	Emery 2008	3.69
	Fernandes 2006	1.89
	Freo 2005	4.87
	Grady 1998	0.89
	Grady 2010	0.26
	Gutchess 2005	2.11
	Kuptsova 2016	4.96
	Langenecker 2003	4.43
	Madden 1997	2.34
	Madden 1999	3.22
	Madden 2010	0.1
	Milham 2002	5.47
	Nyberg 2009	5.19
	Onur 2011	5.03
	Paxton 2007a	2.67
	Podell 2012	5.61
	Prakash 2012	7.21
	Raye 2008	3.36
	Ricciardi 2009	2.43
	Steffener 2016	1.09
	Townsend 2006	6.22
	Zhu 2015	7.29
	Zysset 2007	4.11
young > old	Bloemendaal 2016	36.76
	Carp 2010	21.12
	Grady 1998	0.12
	Paxton 2007a	17.84
	Podell 2012	12.36
	Schulte 2011	11.8
old > young	Anguera 2010	16.91
	Bloemendaal 2016	2.26
	Emery 2008	0.91
	Kuptsova 2016	19.81
	Lamar 2004	17.92
	Madden 2010	3.64
	Paxton 2007b	18.73
	Schulte 2011	14.67
	Zysset 2007	5.03

	Bloemendaal 2016	15.03
	Emery 2008	7.3
	Freo 2005	5.54
	Grady 1998	1.49
	Grady 2010	0.16
	Gutchess 2005	0.49
	Kuptsova 2016	7.59
	Langenecker 2003	3.58
	Madden 1997	2.65
	Madden 1999	9.39
	Nyberg 2009	9.81
	Onur 2011	2.49
	Paxton 2007a	0.16
	Townsend 2006	4.8
	Zhu 2015	18.55
	Zysset 2007	10.78
Performance		
young > old not matched	Bloemendaal 2016	37.19
	Carp 2010	23.92
	Grady 1998	0.19
	Paxton 2007a	22.16
	Podell 2012	16.54
Working Memory		
Pooled	Bäckman 2011	0.49
	Carp 2010	13.76
	Emery 2008	9.18
	Fakhri 2012	0.11
	Freo 2005	13.72
	Grady 1998	2.1
	Gutchess 2005	10.46
	Johnson 2004	0.12
	Madden 1999	2.94
	Nyberg 2009	3.28
	Paxton 2007a	5.6
	Podell 2012	2.09
	Raye 2008	11.79
	Ricciardi 2009	6.37
Without manipulation		
Pooled	Bäckman 2011	9.51
	Carp 2010	18.87
	Fakhri 2012	0.18
	Freo 2005	12.02
	Gutchess 2005	13.53
	Madden 1999	0.39
	Nyberg 2009	5.09
	Paxton 2007a	11.21
	Podell 2012	7.23
	Raye 2008	16.1

	Ricciardi 2009	5.87
Inhibition		
Pooled	Bloemendaal 2016	0.62
	Eich 2016	16.9
	Lamar 2004	28.32
	Onur 2011	1.73
	Paxton 2007b	20.89
	Schulte 2011	14.83
	Zysset 2007	16.7
young > old	Bloemendaal 2016	54.92
	Schulte 2011	45.07
old > young	Bloemendaal 2016	0.76
	Eich 2016	14.83
	Lamar 2004	29.82
	Paxton 2007b	21.44
	Schulte 2011	17.58
	Zysset 2007	15.57

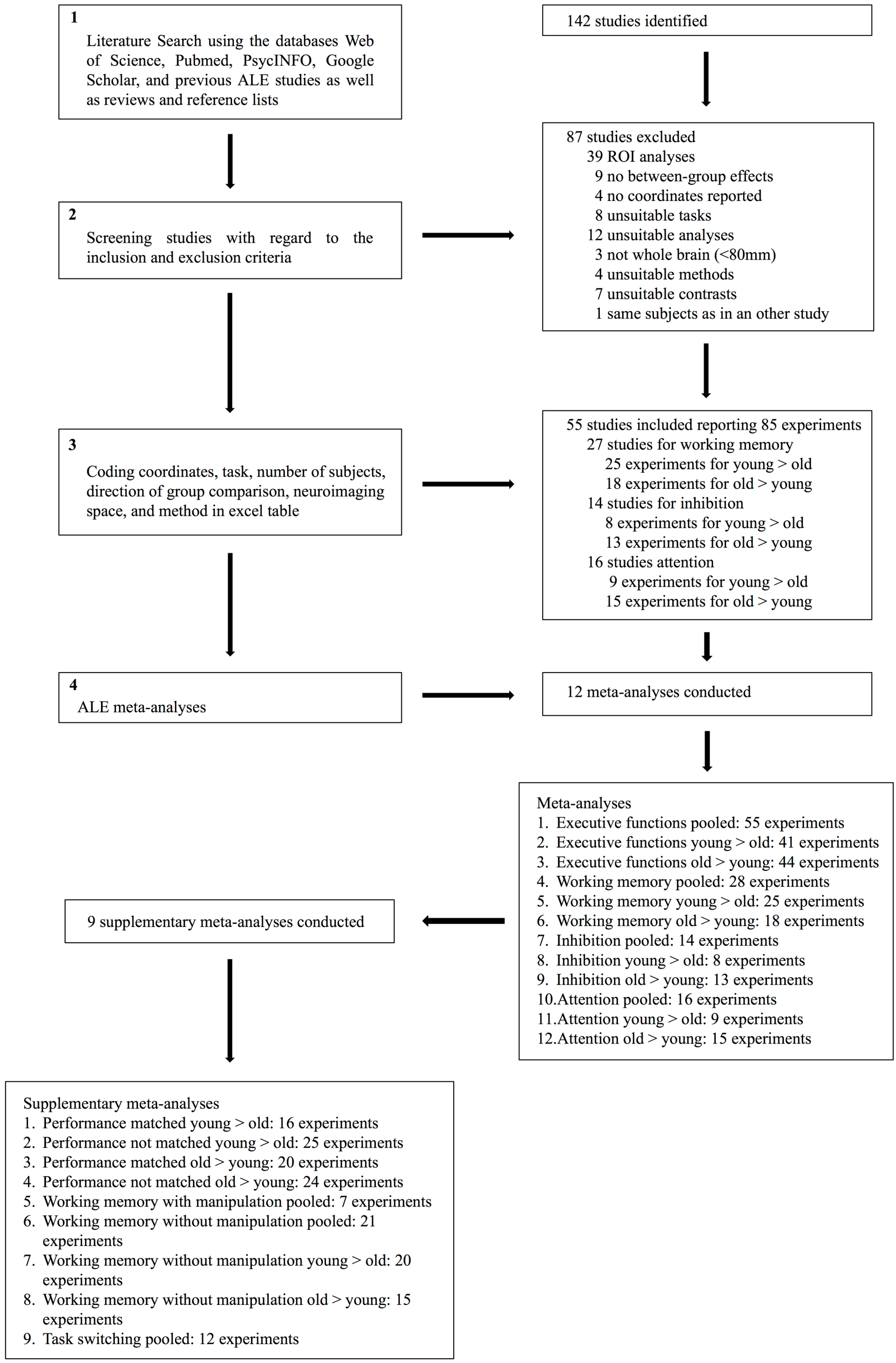

Figure 1. Flowchart of the different steps conducted.

First step

Author	# Subjects	Coordinates (x, y, z)	Space
Example et al.	13	-42, -4, 36	MNI
Example et al.	13	-3, -87, 36	MNI
Example et al.	13	3, 51, 51	MNI
Example et al.	13	45, 18, 54	MNI
Example et al.	13	9, -24, 30	MNI
Example et al.	13	57, -24, -15	MNI
Example et al.	13	48, -57, 54	MNI

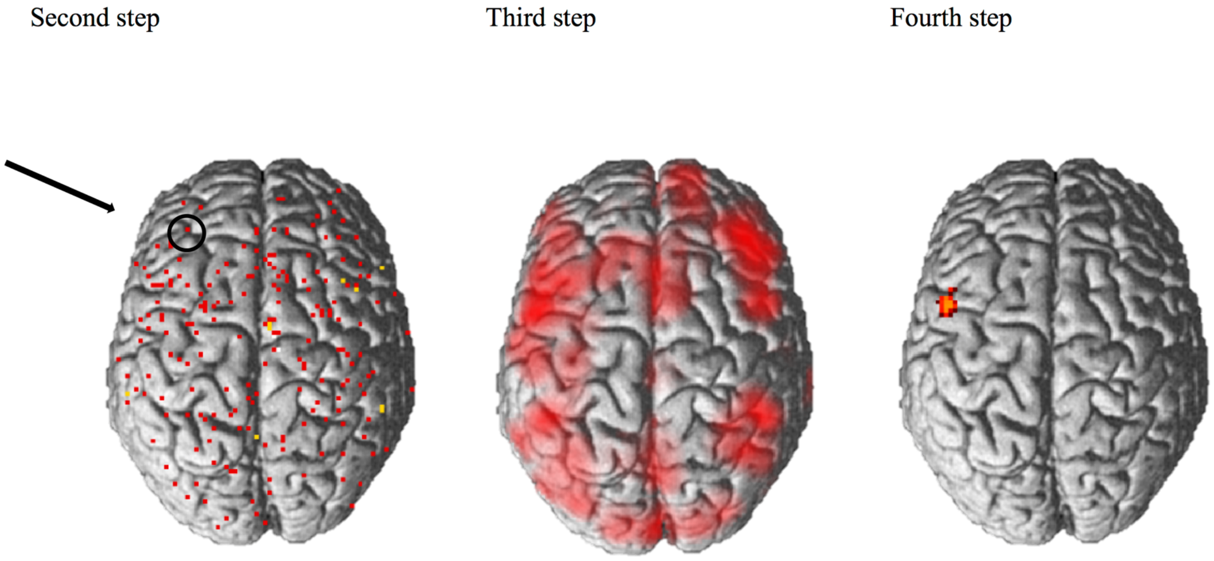

Figure 2. Schematic illustration of the steps of an ALE meta-analysis. In a first step, important content of the included studies is coded in an excel table. In a second step, the reported coordinates of the peak activations, for one experiment, are projected on a brain template for display (as marked for the first coordinates as an example). In a third step, the spatial uncertainty associated with each coordinate is acknowledged by modeling Gaussian probability distributions around each focus. In a fourth step, the probability distributions of all activation foci are combined for each voxel, which results in a modeled activation (MA) map. The union of these MA maps creates voxel-wise ALE scores. These are compared to a null distribution reflecting a random spatial association between experiments.

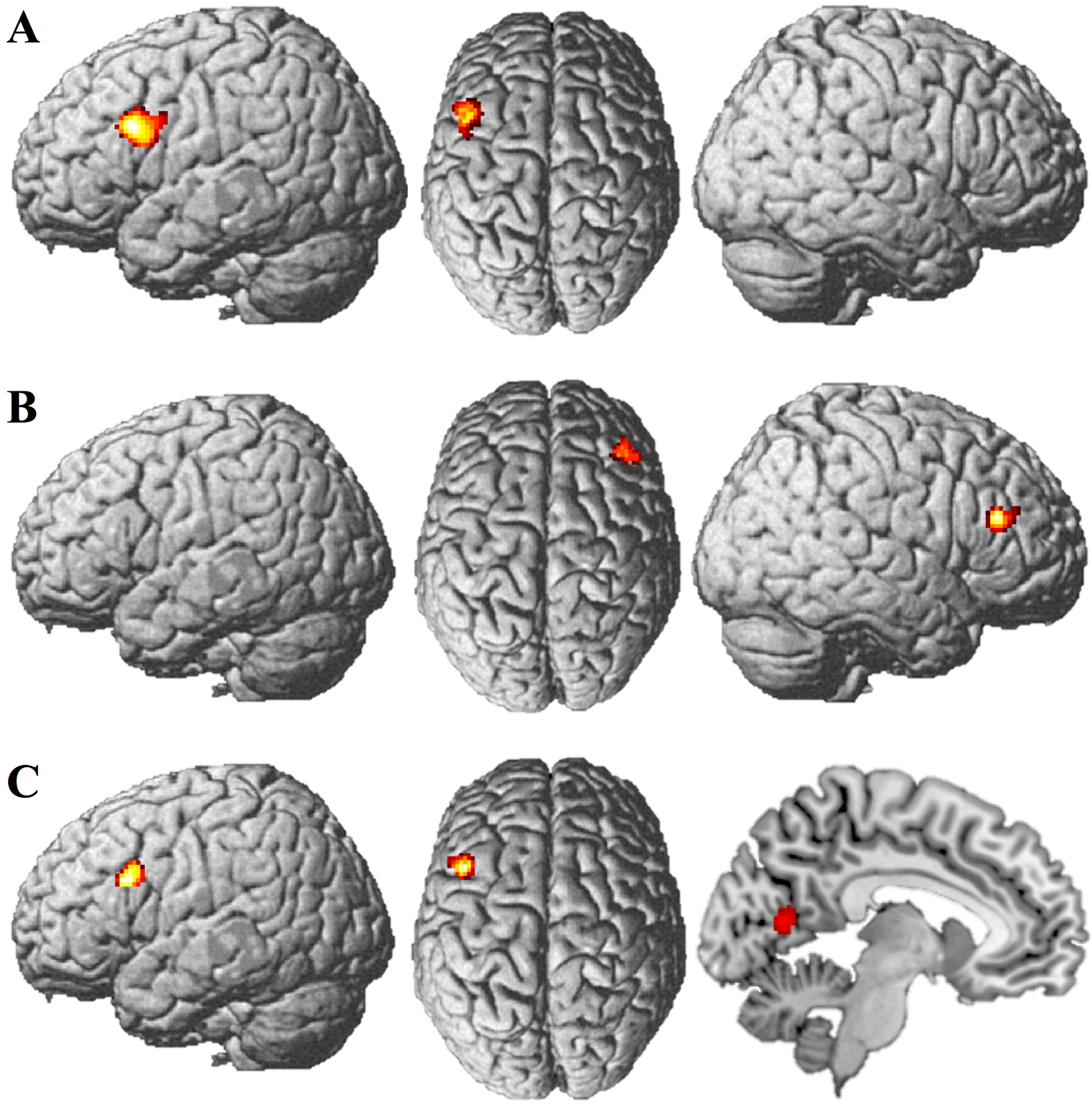

Figure 3. Foci of brain activity showing significant convergence of activity for (A) executive functions pooled, (B) executive functions young > old, and (C) executive functions old > young, (cluster-level $p < .05$, family-wise error-corrected for multiple comparison, cluster forming threshold $p < .001$ at voxel level).

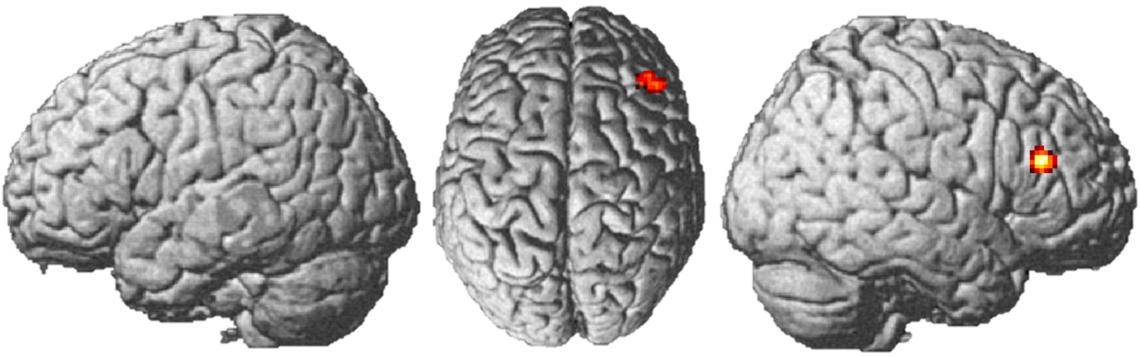

Figure 4. Foci of brain activity showing significant convergence of activity for executive functions young > old performance not matched (cluster-level $p < .05$, family-wise error-corrected for multiple comparison, cluster forming threshold $p < .001$ at voxel level).

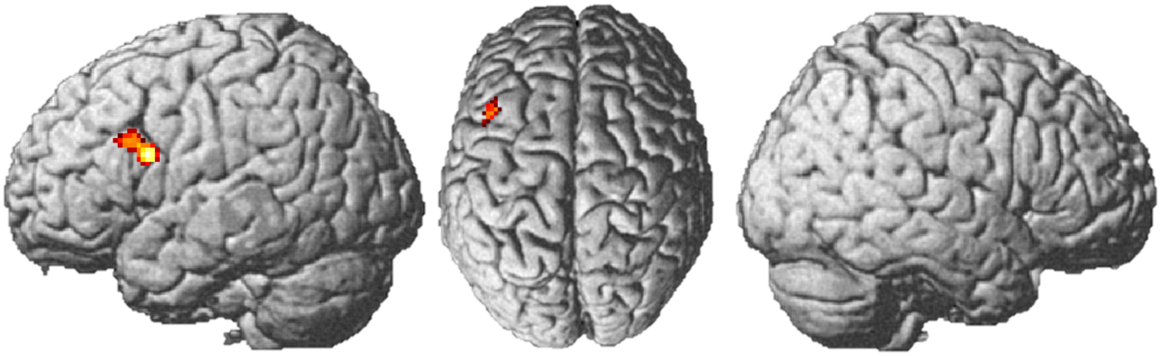

Figure 5. Foci of brain activity showing significant convergence of activity for working memory pooled, (cluster-level $p < .05$, family-wise error-corrected for multiple comparison, cluster forming threshold $p < .001$ at voxel level).

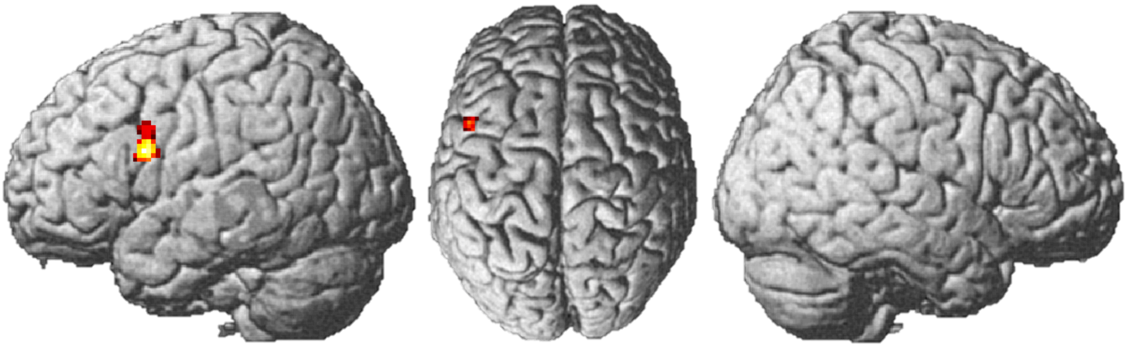

Figure 6. Foci of brain activity showing significant convergence of activity for working memory without manipulation pooled (cluster-level $p < .05$, family-wise error-corrected for multiple comparison, cluster forming threshold $p < .001$ at voxel level).

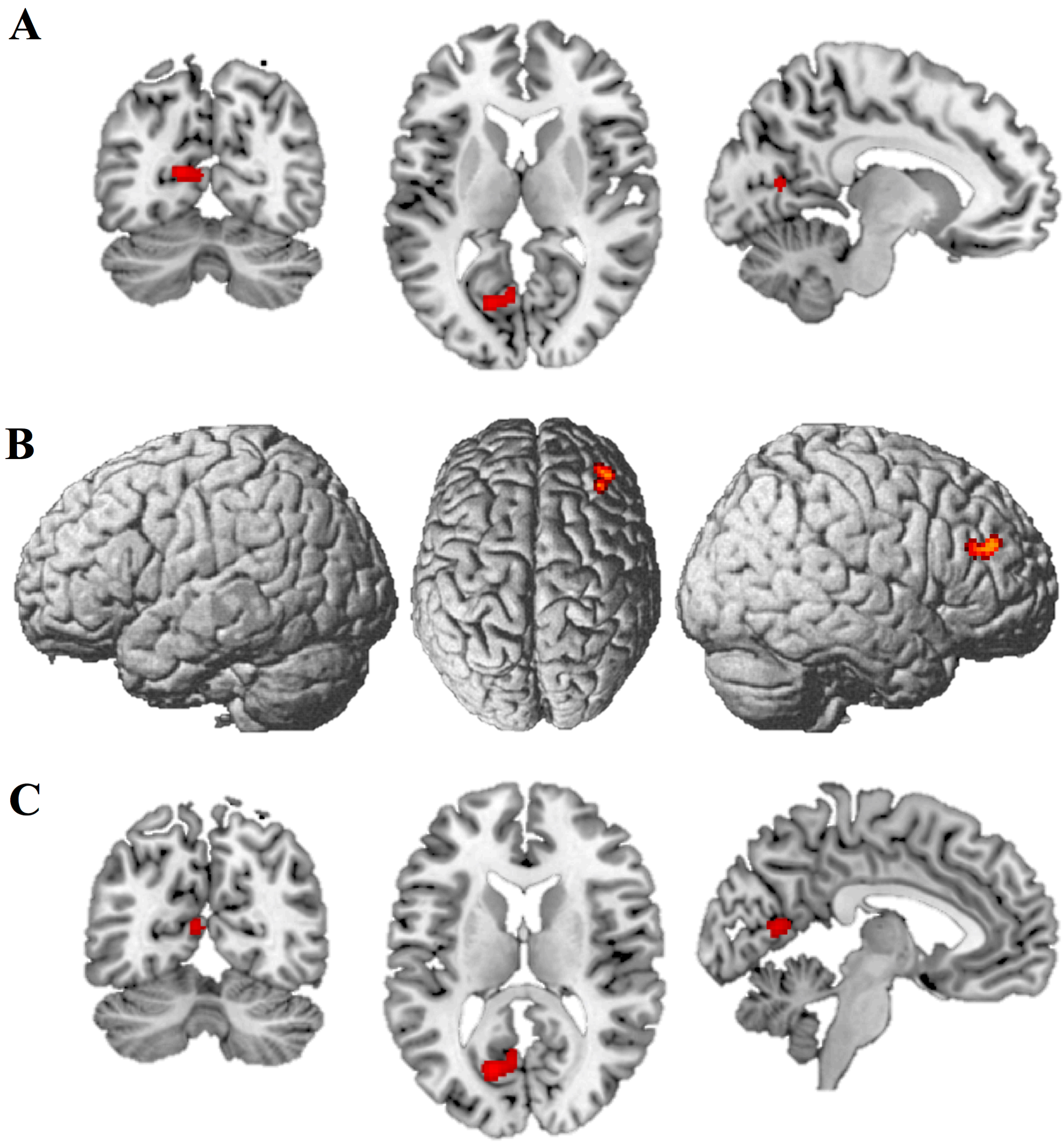

Figure 7. Foci of brain activity showing significant convergence of activity for (A) inhibition pooled, (B) inhibition young > old, and (C) inhibition old > young, (cluster-level $p < .05$, family-wise error-corrected for multiple comparison, cluster forming threshold $p < .001$ at voxel level).

Declaration of Academic Integrity

I, *Marisa Heckner,* hereby confirm that this thesis is solely my own work and that I have used no sources or aids other than the ones stated.

Ort, Datum Unterschrift