



Review article

The effect of task complexity on the neural network for response inhibition: An ALE meta-analysis

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ABSTRACT

Response inhibition is classically investigated using the go/no-go (GNGT) and stop-signal task (SST), which conceptually measure different subprocesses of inhibition. Further, different task versions with varying levels of additional executive control demands exist, making it difficult to identify the core neural correlates of response inhibition independent of variations in task complexity. Using neuroimaging meta-analyses, we show that a divergent pattern of regions is consistently involved in the GNGT versus SST, arguing for different mechanisms involved when performing the two tasks. Further, for the GNGT a strong effect of task complexity was found, with regions of the multiple demand network (MDN) consistently involved particularly in the complex GNGT. In contrast, both standard and complex SST recruited the MDN to a similar degree. These results complement behavioral evidence suggesting that inhibitory control becomes automatic after some practice and is performed without input of higher control regions in the classic, standard GNGT, but continues to be implemented in a top-down controlled fashion in the SST.

1. Introduction

Executive functions (EF) refer to a complex set of top-down control processes which allow us to process current objectives and to reevaluate and adjust our behavior according to changing environmental conditions (Jurado and Rosselli, 2007). Together with working memory and cognitive flexibility, inhibitory control has been suggested to be one of the key components of EF (Diamond et al., 2013; Niendam et al., 2012). Under the rubric of inhibitory control two major components have been proposed: response inhibition (i.e., the ability to suppress or cancel prepotent but inappropriate motor reactions), and attentional inhibition (i.e., the ability to resist interference from stimuli in the external environment (Friedman and Miyake, 2004; Diamond, 2013; Tiego, 2018). Response inhibition thus is crucial for self-control (cf. Diamond et al., 2013; Langner et al., 2018). If we want to cross the street but at the exact same moment the light changes from green to red, we need to be able to detect this environmental change to discard the tendency to walk on and to stop our current action plan. In order to investigate the process of response inhibition, most functional magnetic resonance imaging (fMRI)

studies have relied on two classic response inhibition tasks: the go/no-go task (GNGT) and the stop-signal task (SST) (Diamond et al., 2013; Aron et al., 2007a; Senderecka et al., 2012; Jonkman et al., 2003; Wöstmann et al., 2013). In the classic GNGT participants are instructed to respond to a go stimulus and to withhold their motor response if a no-go stimulus is presented. Usually, the proportion of go stimuli is much higher than the proportion of no-go stimuli to achieve a strong prepotency towards responding (Donders et al., 1969). In contrast, the stop-signal task investigates the cancellation of an already initiated motor response (Logan et al., 1984). Similar to the go/no-go task participants are asked to respond as quickly as possible to a go stimulus. However, in some trials, a stop-signal is presented briefly after the go stimulus telling the participant to cancel the motor response.

Even though both tasks probe conceptually different aspects of response inhibition, that is response withholding versus action cancellation, inhibitory control has often been investigated by pooling together results from both tasks (e.g. Puu et al., 2020; Hung et al., 2018). Interestingly, a behavioral study showed performance in GNGT and SST to load on a single factor (Bender et al., 2016). Other behavioral

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studies, however, suggested that the SST triggers controlled inhibition, while the standard GNGT, if using a consistent stimulus–response (S-R) mapping, can be operated through automatic inhibitory processes once S-R contingencies have been learned (Verbruggen and Logan, 2008a; b). Schachar et al. (2007, 2011) developed an adapted version of the SST to overcome limitations of the standard go/no-go task and be able to investigate action withholding versus action cancellation within one paradigm. They found that patients with ADHD show deficits in both aspects of inhibitory control. Studies focusing on a potential interaction between emotions and inhibition, revealed that negative affective stimuli affect performance in the SST but not in the GNGT, providing further evidence that the two tasks rely on different mechanisms (Littman and Takács, 2017). Pharmacological investigations also suggest different anatomic and chemical modulations involved in the two tasks (Eagle et al., 2008).

Functional neuroimaging studies commonly reported a network consisting of the dorsolateral prefrontal cortex (DLPFC) and inferior frontal gyrus (IFG), as well as additional activation within the anterior midcingulate cortex (aMCC), pre-supplementary motor area (preSMA), anterior Insula (aI), inferior parietal lobe (IPL), intraparietal sulcus (IPS) and the basal ganglia to be involved in response inhibition (e.g. Aron et al., 2011; Garavan et al., 1999; Steele et al., 2013). However, single fMRI studies as well as neuroimaging meta-analyses have also revealed some differences in the neural correlates of the two tasks (e.g. Cieslik et al., 2015; Sebastian et al., 2013a; b), especially within the lateral prefrontal cortex and the parietal lobe. Moreover, a host of fMRI studies have reported mainly right-hemispheric activations (Garavan et al., 1999; Kawashima et al., 1996; Konishi et al., 1998; Aron et al., 2004; Aron et al., 2014) in these tasks, but only few studies have performed direct comparisons between the hemispheres (but see some exceptions, e.g. Aron and Poldrack, 2006; Cai and Leung, 2009). On the other hand, there are also numerous fMRI studies reporting bilateral prefrontal activations for the GNGT (Baumeister et al., 2014; Watanabe et al., 2002; Rubia et al., 2001; Liddle et al., 2000) and the SST (Berkman et al., 2014; Cai and Leung et al., 2009; Rubia et al., 2001; Schel et al., 2014; Leunissen et al., 2016; Congdon et al., 2014), questioning the theory of a right-lateralization of the response inhibition network.

The picture is complicated by the fact that many different variations of these two tasks have evolved over time, with varying levels of involvement of other EF aspects, such as increased WM demands or anticipation effects, leading to increased task complexity and, hence, an involvement of different or additional brain regions. These variations have made it difficult to identify the key neural correlates of inhibitory control. While some authors support the theory of a bilateral response inhibition network (Mazzola-Pomietto et al., 2009; Schel et al., 2014; Tabu et al., 2012), others have argued that the activity in left lateral frontal cortex may not be directly associated with response inhibition but rather result from differences in task design (Rubia et al., 2001; Watanabe et al., 2002; Fassbender et al., 2004), the contrasts used to isolate the inhibition process (Watanabe et al., 2002; Rubia et al., 2001), or the processing of salient cues (like a rare no-go or stop stimulus; Fuentes-Claramonte et al., 2016). Likewise, differences in efficiency of response inhibition (Hirose et al., 2012) or task difficulty (Bellgrove et al., 2004) have been discussed as potential reasons for left-hemispheric involvement.

Different research groups have already used neuroimaging meta-analyses to investigate the core neural network consistently involved in the two tasks, irrespective of different task implementations. This line of research started with Nee and colleagues (Nee et al., 2007), who, while acknowledging that both tasks are conceptually different, performed a meta-analysis across both paradigms due to a limited number of studies. Simmonds et al. (2008) went on to examine the effect of task complexity on GNGT-related brain activity, albeit based on only a small number of studies, providing first evidence that particularly the complex versions recruit a fronto-insula-parietal network, while this does not seem to be the case for standard task versions. Not considering task

complexity, Swick et al. (2011) focused on differences between GNGT and SST and found that the GNGT recruits the frontoparietal network to a greater extent, while the SST leads to more involvement of the cingulo-opercular network. While not focusing specifically on differences between the two tasks, a meta-analysis of our own group confirmed this finding (Cieslik et al., 2015). Levy and colleagues (Levy et al., 2011) investigated the effect of stimulus probability in inhibitory control, by pooling together GNGT and SST experiments with rare no-go or stop-signal stimulus probabilities and comparing the results to a meta-analysis of the GNGT using equiprobable go and no-go stimuli. They found that both analyses yielded convergence in right middle frontal gyrus and anterior insula. Furthermore, posterior ventrolateral PFC (VLPFC) revealed convergence only when inhibition trials were rarely presented, while mid-VLPFC showed convergence for equiprobable stimulus presentation in the GNGT, i.e., when there is increased uncertainty of which response has to be made. In a critical review and meta-analysis of the GNGT, Criaud and Boulinguez (2013) evaluated the influence of different complexity levels, specifically the effect of stimulus complexity, no-go probability, as well as working memory load. They argued that most parietal and prefrontal regions showing convergence in the GNGT are actually not specialized for inhibitory control but rather associated with more general functions, such as attentional processing or maintaining relevant information in working memory. Later on, Zhang et al. (2017) reported separate meta-analyses on interference resolution, action withholding (GNGT), and action cancellation (SST). Furthermore, they conducted several sub-analyses, including a comparison of high (~ 50% no-go stimuli) vs. low probability (< 50% no-go stimuli) no-go conditions and a comparison of SST and GNGT, both of which did not show any significant differences. Finally, one of the most recent meta-analyses on inhibitory control (Ishewood et al., 2021) emphasized the importance of subcortical regions in response inhibition and inference resolution, revealing a crucial role of the putamen for inhibitory control. Taken together, although there is already quite some meta-analytic work comparing the GNGT and SST, the results are diverging, possibly due to the different numbers and varieties of included experiments and the fact that some analyses have taken complexity into account and others have not. However, there is evidence for a strong effect of task complexity on the network involved in the GNGT, while this has not been examined in the SST yet. In particular, divergent results across meta-analyses might be due to interactions between task type (GNGT, SST) and complexity (standard /complex task).

In general, brain regions involved in the GNGT and SST have also been found to be recruited in tasks probing other EFs (Duncan, 2010; Camilleri et al., 2018), such as WM (Rottschy et al., 2012) or task switching (Worringer et al., 2019). Therefore, this domain-general fronto-insular-parietal network is commonly referred to as the multiple-demand-network (MDN) (Duncan and Owen, 2000; Duncan, 2010; Fedorenko et al., 2013). While there is evidence that the MDN is recruited whenever a difficult condition, potentially demanding a higher degree of top-down control, is contrasted against an easier one, such as high versus low working memory load or response-conflict versus no-conflict trials, it is still not clear how exactly this network is modulated by increasing task complexity. On the one hand, there is evidence that the MDN is recruited in a progressive fashion with more posterior regions of the network (i.e., IPS, preSMA and posterior lateral frontal cortex) already involved in easy tasks, whereas more anterior frontal regions and aI are only recruited when complexity, time pressure, or reward increases (Shashidhara et al., 2019). On the other hand, there is also evidence showing that increasing task complexity leads to quantitative rather than qualitative changes in MDN recruitment. Crittenden and Duncan (Crittenden and Duncan, 2014) used a relatively easy visual discrimination task and manipulated task complexity in three ways. Importantly, all manipulations of complexity led to activation within the MDN, with increases in activity with increasing complexity, suggesting that the MDN is recruited as a whole even by comparatively simple tasks

(cf. Crittenden and Duncan, 2014). Thus, there is little and inconsistent information on the effects of task complexity on the recruitment of the MDN and on the question of whether task complexity leads to qualitative changes (in particular, more anterior activation with increased task complexity) or, rather, to quantitative changes (stronger activation within MDN regions but not additional regions coming into play with increased task complexity).

The aim of the current meta-analysis is to investigate if action withholding and action cancellation as measured by the GNGT and SST respectively share a common response inhibition network and if there is a (differential) modulation by task complexity. While previous neuroimaging (meta-analytic) evidence suggests that there is a relevant effect of task complexity on the network recruited by the GNGT, this has not yet been investigated in the SST. We therefore aimed to compare the network recruited in standard versus complex versions of the GNGT and SST, respectively. Furthermore, if there is an effect of task complexity, how does task complexity modulate the recruitment of the MDN in these two paradigms? Does increased task complexity lead to quantitative changes in MDN recruitment, as reflected in the same neural network being involved in both standard and complex versions? Or is increased task complexity reflected in qualitative changes, so that complex versions show additional convergence of particularly more anterior frontal regions, as compared to standard task versions? To this end, we used coordinate-based activation likelihood estimation (ALE) meta-analyses (Eickhoff et al., 2012; Eickhoff et al., 2009; Turkeltaub et al., 2012) and conducted separate meta-analyses of neuroimaging studies on GNGT and SST to identify the core neural correlates of action withholding and action cancellation, respectively. Importantly, we also performed separate meta-analyses for both tasks differentiating between the classic, i.e. standard, task design (using standard or symbolic stimuli such as letters, geometrical shapes or colored stimuli) and complex task design (e.g. paradigms with additional increased WM demand or complex stimuli such as faces or battleships). This enabled testing if increased task complexity leads to quantitative or rather qualitative changes within the associated neural networks consistently involved in GNGT and SST. Conjunction analyses were conducted across standard versions of the GNGT and SST and across complex versions, respectively, to test for a common neural network associated with response inhibition and general effects of task complexity across the two paradigms. We hypothesized that if both tasks probe similar aspects of response inhibition a very similar set of regions should be found in the meta-analysis for standard GNGT and standard SST. Moreover, if task complexity leads to quantitative changes in neuronal recruitment, standard and complex versions should recruit the same neural network, while qualitative changes should be reflected in additional convergence of particularly more anterior frontal regions for the complex task versions.

2. Methods

2.1. Selection criteria for the experiments included in the meta-analysis

Since this meta-analytic study focused on the neural correlates of response inhibition, we included the two most commonly tasks used to investigate the exertion of inhibitory control, the GNGT and the SST. Our meta-analyses were conducted according to the standards of our institute (cf. e.g. Cieslik et al., 2015; Müller et al., 2017) and followed the guidelines for conducting coordinate-based neuroimaging meta-analyses as outlined in Müller et al. (2018).

To identify eligible experiments, we performed a PubMed database (<https://pubmed.ncbi.nlm.nih.gov/>) search using the following search strings: “go/no-go task”, “stop-signal task”, “response inhibition / action inhibition / motor inhibition / inhibition / inhibitory control”, “action cancellation” “action withholding” together with either “fMRI” or “neuroimaging”; the Google Scholar database was queried using the same search strings. Additional studies were obtained by reference tracing of already identified studies and comparison with a previous

meta-analysis from our group (Cieslik et al., 2015) as well as other meta-analyses on response inhibition (Simmonds et al., 2008; Swick et al., 2011; Criaud et al., 2013; Puiu et al., 2020; Hung et al., 2018; Ardila et al., 2018; Zhang et al., 2017; Levy et al., 2011; Nee et al., 2007). We furthermore contacted authors to retrieve additional results if the outcome of the contrast of interest was not included in the publication. Further information about the search steps and exclusion criteria can be found in the flowchart shown in Fig. 1.

A checklist used here as a guidance for neuroimaging meta-analyses as recommended by Müller et al. (2018) can be found in table S1.

Only whole-brain fMRI analyses reporting peak activation coordinates in a standard reference space – Montreal Neurological Institute (MNI) or Talairach-Tournoux (TAL) system – were considered for inclusion. Reported coordinates of experiments using FSL or SPM were treated as MNI coordinates as this is the standard space in these softwares. Only in cases when authors explicitly reported a transformation of MNI in TAL space, the coordinates were considered to be in TAL space when using FSL or SPM. Otherwise, the coordinate space was treated as MNI (cf. Müller et al., 2018). Results from region-of-interest analyses were excluded. Likewise, results from fMRI studies in which only part of the brain was scanned were also excluded.

We included data from healthy adults (≥ 18 years old) without any diagnosed neurological or psychiatric diseases, while data from children, patients as well as healthy subjects with increased risk for neurological or psychiatric disorders, such as healthy relatives, were discarded. When patient studies reported the results of the control and patient groups individually, the results from the healthy control group were included. Moreover, data from pharmacology or transcranial magnetic stimulation studies were excluded, even if the coordinates of the sham/placebo group were separately published, in order to avoid the potential influence of anticipation effects on the results.

With respect to the contrasted task conditions, we only included contrasts representing increased cognitive control during the inhibition condition as compared with an active control condition, i.e. no-go > go and stop > go trials. The reverse contrast (i.e. go > no-go or go > stop, representing deactivations) as well as inhibitory effects compared with a resting baseline (e.g. no-go > rest or stop-signal > rest) were excluded. However, in some experiments, only no-go trials were explicitly modeled for analysis, while brain activity during go trials was not modeled explicitly but included in the implicit baseline. Here, the contrast no-go > active baseline was included in our meta-analysis, as we considered such contrasts rather comparable with no-go > go contrasts. In order to account for differences in the coordinate space, the coordinates of experiments reported in the TAL system were converted into MNI using linear transformation (Lancaster et al., 2007).

When a publication reported several eligible contrasts for the same task (for example, when both standard and complex task versions were used in the same sample), the results reported for the different contrasts were pooled into one experiment for the overall analysis (e.g. Ko et al., 2016; Czapla et al., 2017). This was done in order to prevent a single study group from having a predominant effect on our results (Turkeltaub et al., 2012). Experiments taken from the same publication which reported coordinates obtained from different participants (e.g. two different age groups) were not pooled. Finally, when a given sample was used in different publications, only one of the publications and its corresponding experiments were included in our analysis to avoid systematic biases induced by one particular study sample (e.g. Sebastian et al., 2016, 2017; van der Meer et al., 2011; 2013).

As we were specifically interested in the cognitive processes taking place when inhibiting a prepotent motor response, we decided to only include experiments using an event-related design. It has been suggested that event-related designs are better suited to capture the specific activity related to response inhibition during no-go trials (cf. Criaud et al., 2013). Already Liddle and colleagues (Liddle et al., 2000) suggested that block designs are not optimal to isolate brain activity specifically related to response inhibition but rather also include aspects of decision making

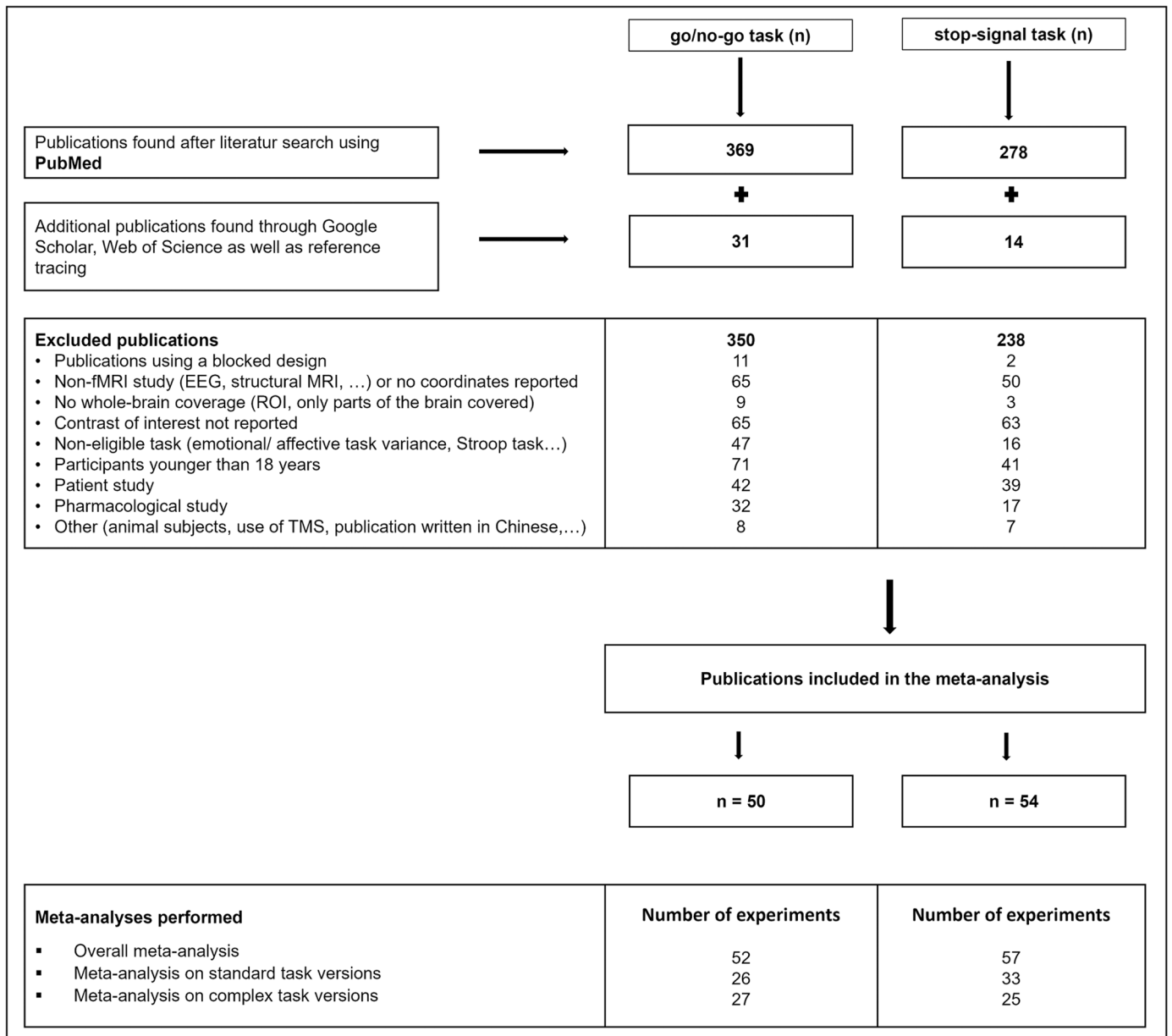


Fig. 1. Flowchart of the search steps and exclusion criteria used in the literature search. Abbreviations: fMRI: functional magnetic resonance imaging, EEG: electroencephalography, MRI: magnetic resonance imaging, ROI: region of interest, TMS: transcranial magnetic stimulation.

and monitoring. As go blocks require low decision making demands compared to mixed go/no-go blocks where participants have to choose between two response options, contrasting no-go with go blocks most likely also reflects aspects of decision making and monitoring rather than pure response inhibition.

2.2. Definition of standard versus complex task versions

Similar to Simmonds et al. (2008), we categorized those versions of the GNGT or SST as standard that used one or more specific stimuli as a go signal (e.g., the letter O for go in the GNGT, or left vs. right pointing arrows as go stimuli in the SST) and another stimulus as no-go or stop-signal (e.g., the letter X for withholding responses in the GNGT or an acoustic stop signal in the SST). If the standard paradigm was adapted to the effect that additional processing demands were needed to process the task at hand, the given experiment was categorized as complex. In particular, if the experiment used a combination of two tasks (e.g. a flanker task and GNGT, e.g. Baumeister et al., 2014), included a switch

component or an additional rare/ oddball go stimulus (e.g. Kenner et al., 2010 and McNab et al., 2008), or when the correct response depended on whether the stimulus was presented in an alternating or non-alternating manner (Garavan et al., 1999), the experiment was categorized as complex as these task variations most likely lead to more complex S-R associations, higher working memory load, or a need for increased attentional control. A recent behavioral study demonstrated that additional cognitive processing negatively affects inhibitory control: higher working memory load resulted in longer stop-signal reaction time (Boucher et al., 2020). Additionally, task versions such as the moving bar stop-signal task – an anticipatory stop-signal task – were classified as complex, because such alternative designs may prompt additional activation in regions related to attentional control (see Zandbelt et al., 2010).

Tasks were also labeled as complex when they did not employ the standard, classically used stimuli as go and no-go or stop-signals (e.g., letters, shapes, tones etc.) but employed starkly different and visually more complex stimuli (e.g., bombs or airplanes, elaborate pictures or

faces). The reason behind this approach was that recent studies have shown that complex stimuli lead to stronger activation and workload within visual short-term working memory than do more basic stimuli (Luria et al., 2010) and that increased visual complexity can also trigger emotional, perceptual, and semantic processing dependent on aspects such as coloring and realism (Schlochtermeyer et al., 2013). Furthermore, an investigation regarding phobic and threatening stimuli suggested that due to the automatic emotional processing of these stimuli, additional activation in regions such as the amygdala can be expected, which may interfere with, for instance, perceptual learning processes (Schmidt et al., 2011). In regard to this, some of the stimuli used in GNG paradigms, such as airplanes and bombs (see Rubia et al., 2001), superheroes/ villains (see Meffert et al., 2016) or battlefield scenarios (see Chikara et al., 2018) could also be considered as threatening. As alluded to above, Littman and Takács (2017) recently showed that the use of negative emotional stimuli impairs performance in the SST. Based on the above-mentioned possible interactions between more complex or emotionally charged stimuli and response inhibition processes, we included experiments with that kind of stimuli in the complex category. In Tables S8b and S9b, we provide a short description of each paradigm, together with a label indicating if the paradigm was standard (“S”) or if it carried increased complexity on the stimulus (“C-stimulus”) or task (“C-task”) level, or both (“C-both”).

2.3. Number of experiments included

Based on these inclusion and exclusion criteria, 50 studies with 52 individual go/no-go experiments were identified to be eligible for the main analysis. For the meta-analyses focusing on task complexity, 26 standard and 27 complex go/no-go experiments were included. For more information regarding the GNGT experiments included, please see Tables S8a-c. Likewise, 54 studies with 57 individual SST experiments were included in the SST main analysis. For the meta-analysis on the standard SST, 33 experiments were included, while 25 experiments were included in the complex SST meta-analysis. For more information regarding the SST experiments included, please see Tables S9a-c.

2.4. Activation likelihood estimation

To identify areas showing significant convergence across experiments, we conducted ALE meta-analyses (Eickhoff et al., 2012; Eickhoff et al., 2009; Laird et al., 2009a; Laird et al., 2009b; Turkeltaub et al., 2002) according to the standard procedures of our institute (e.g. Langner and Eickhoff, 2013; Rottschy et al., 2012). ALE models the coordinates as centers of 3-D Gaussian probability distributions instead of single foci in order to account for the spatial uncertainty of each single focus. The width of the Gaussian probability distribution is based on empirical data on between-subject and between-template variance and adjusted accordingly. A higher number of subjects reflects greater reliability and thus the Gaussian curve is modeled tighter, while a smaller number of subjects is modeled by a wider and lower Gaussian curve (Eickhoff et al., 2009).

The distribution probabilities of all foci in a given experiment were combined for each voxel and a modeled activation (MA) map derived (Turkeltaub et al., 2012). At the next step, a union MA map was calculated across all individual MA maps of the experiments included, resulting in voxel-wise ALE scores that reflect the convergence of results across experiments at each location of the brain. To identify ‘true’ from ‘random’ convergence across experiments, ALE scores were compared against an empirical null-distribution that reflects random spatial association between experiments. This null-distribution was created by taking a voxel at random from each of the individual MA maps and taking the union of these values in the same manner as done for the spatially contingent voxels in the true analysis, which was then repeated 10,000 times.

The p-value of the “true” ALE is then derived by the proportion of

equal or higher values obtained under the null-distribution. The resulting non-parametric p-values for each individual meta-analysis were thresholded at cluster-level $p < 0.05$, family-wise error-corrected for multiple comparisons, with a cluster-forming threshold at voxel level of $p < 0.001$, and then transformed into z-scores for display. Conjunction analyses were performed by using the conservative minimum statistic (Nichols et al., 2005) to identify voxels that showed a significant effect in each of the individual meta-analyses. A detailed description of the contrast analysis is provided in the [supplementary material](#).

The resulting coordinates were anatomically labeled by reference to the SPM Anatomy Toolbox, version 3.0 (Eickhoff et al., 2007; Eickhoff et al., 2005). Please see Tables S2 -S7 for a full overview of the study contributions.

3. Results

3.1. Action withholding

3.1.1. General analysis across go/no-go experiments independent of task complexity ($n = 52$)

The general meta-analysis across all experiments using an event-related GNGT version, independent of task complexity, revealed consistent activity in bilateral IPS and inferior parietal cortex (IPC), left lateral occipital cortex, the right superior temporal sulcus (STS) extending into right middle temporal gyrus (MTG), anterior midcingulate cortex (aMCC), pre-supplementary motor area (preSMA) extending into SMA, bilateral aI, right inferior frontal junction (IFJ), and right mid-DLPFC. Subcortical convergence was found in bilateral putamen (Fig. 2A, Table S10).

3.1.2. Standard go/no-go experiments ($n = 26$)

The meta-analysis across experiments using a standard event-related GNGT version revealed consistent activity in bilateral lateral occipital cortex (in particular hOc41a), right STS, right IPC (area PGa), preSMA/SMA, and right aI (Fig. 2B, Table S11).

3.1.3. Complex go/no-go experiments ($n = 27$)

The meta-analysis across complex event-related GNGT experiments revealed consistent activity in right IFG (pars opercularis), bilateral aI extending into putamen, right IFJ and right mid-DLPFC as well as a cluster covering anterior DLPFC (aDLPFC) extending into the frontal pole, right superior occipital cortex extending into superior parietal lobule (SPL), bilateral IPS and anterior midcingulate cortex (aMCC) (Fig. 2C, Table S12).

Importantly, the meta-analyses on standard versus complex GNGT versions included a comparable number of experiments (i.e., 26 versus 27 experiments, respectively), ruling out the possibility that differences in the network involved were simply driven by a different number of included experiments.

3.2. Action cancellation

3.2.1. General analysis of stop-signal task experiments independent of task complexity ($n = 57$)

The general meta-analysis across experiments using an event-related SST version, independent of task complexity, revealed consistent activity in bilateral aI extending into IFG (pars opercularis / triangularis) in the right hemisphere, in right DLPFC, right dorsal premotor cortex (dPMC), aMCC extending into preSMA, bilateral temporoparietal junction (TPJ) zone extending from IPC into bilateral middle temporal gyrus, bilateral IPS, and bilateral IFJ extending into precentral gyrus. Subcortical convergence was found in right caudate nucleus and right thalamus (Fig. 3A, Table S13).

3.2.2. Standard stop-signal task experiments ($n = 33$)

The meta-analysis of standard event-related SST experiments

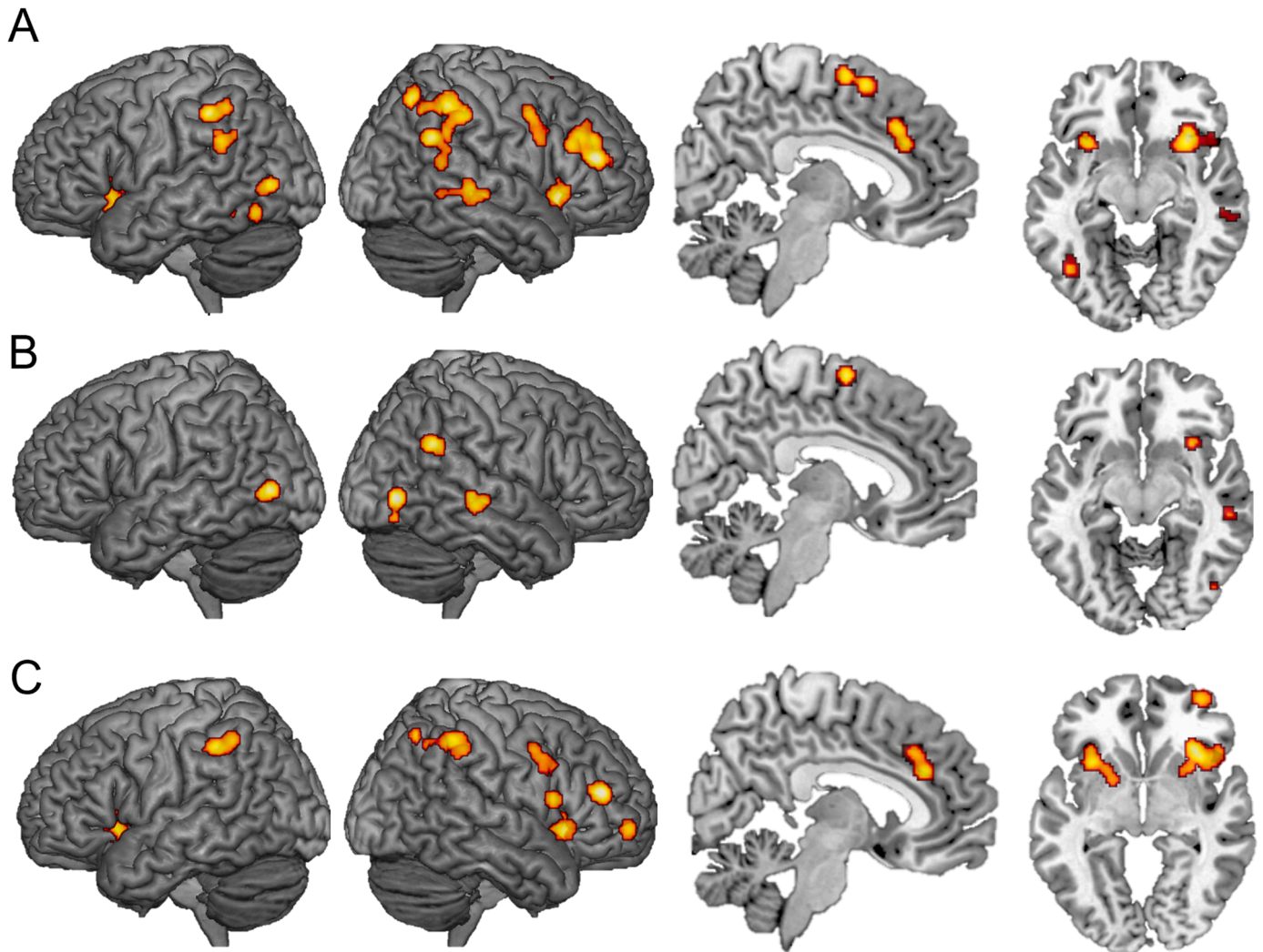


Fig. 2. Meta-analyses across go/no-go task experiments. Brain regions showing significant convergence of brain activity (cluster-level $p < 0.05$ family-wise error-corrected for multiple comparisons, cluster-forming threshold $p < 0.001$ at voxel level) across event-related fMRI experiments including (A) all go/no-go task experiments independent of task complexity, (B) only experiments with standard go/no-go task versions, and (C) only experiments with complex go/no-go task versions.

revealed convergence in bilateral TPJ, spanning from IPC over superior temporal gyrus (STG) into STS, left IPC (area PFcm, PFm), right IPS, right dPMC, aMCC extending into preSMA, bilateral aI extending into IFG (pars opercularis/ triangularis) in the right hemisphere, and right DLPFC. Subcortical convergence was found in right caudate nucleus (Fig. 3B, Table S14).

3.2.3. Complex stop-signal task experiments ($n = 25$)

The meta-analysis of complex event-related SST experiments revealed convergence in bilateral TPJ, aMCC/ pre-SMA, bilateral aI extending into IFG (pars opercularis/ triangularis) in the right hemisphere, and bilateral IFJ extending into precentral gyrus on the left side. Subcortical convergence was found in right thalamus (Fig. 3C, Table S15).

3.3. Commonalities of Action withholding and Action cancellation

3.3.1. Conjunction analysis across standard go-/no-go experiments and standard stop-signal experiments

The conjunction analysis across the ALE maps of the standard GNGT and standard SST revealed convergence in right aI and right STS (Fig. 4A).

3.3.2. Conjunction analysis across complex go-/no-go experiments and complex stop-signal experiments

The conjunction analysis across the complex GNGT and complex SST revealed convergence in bilateral aI, aMCC, and right IFJ (Fig. 4B).

The results of the meta-analytic contrasts between standard GNGT and standard SST and between complex GNGT and complex SST, respectively, are provided in the [supplementary material](#) (Fig. S1 and S2).

4. Discussion

In this series of ALE meta-analyses, we investigated the commonalities and differences between the go/no-go and stop-signal tasks and to which degree regions of convergence are affected by task complexity. While results of both tasks have often been pooled together when discussing the neural correlates of response inhibition, our results revealed a divergent pattern of brain regions consistently involved in standard GNGT versus standard SST, providing evidence for different underlying mechanisms. Further, task complexity strongly affected the pattern of regions involved in withholding responses in no-go trials, with key regions of the MDN particularly recruited in the complex task version. In contrast, no such pronounced difference was found for canceling

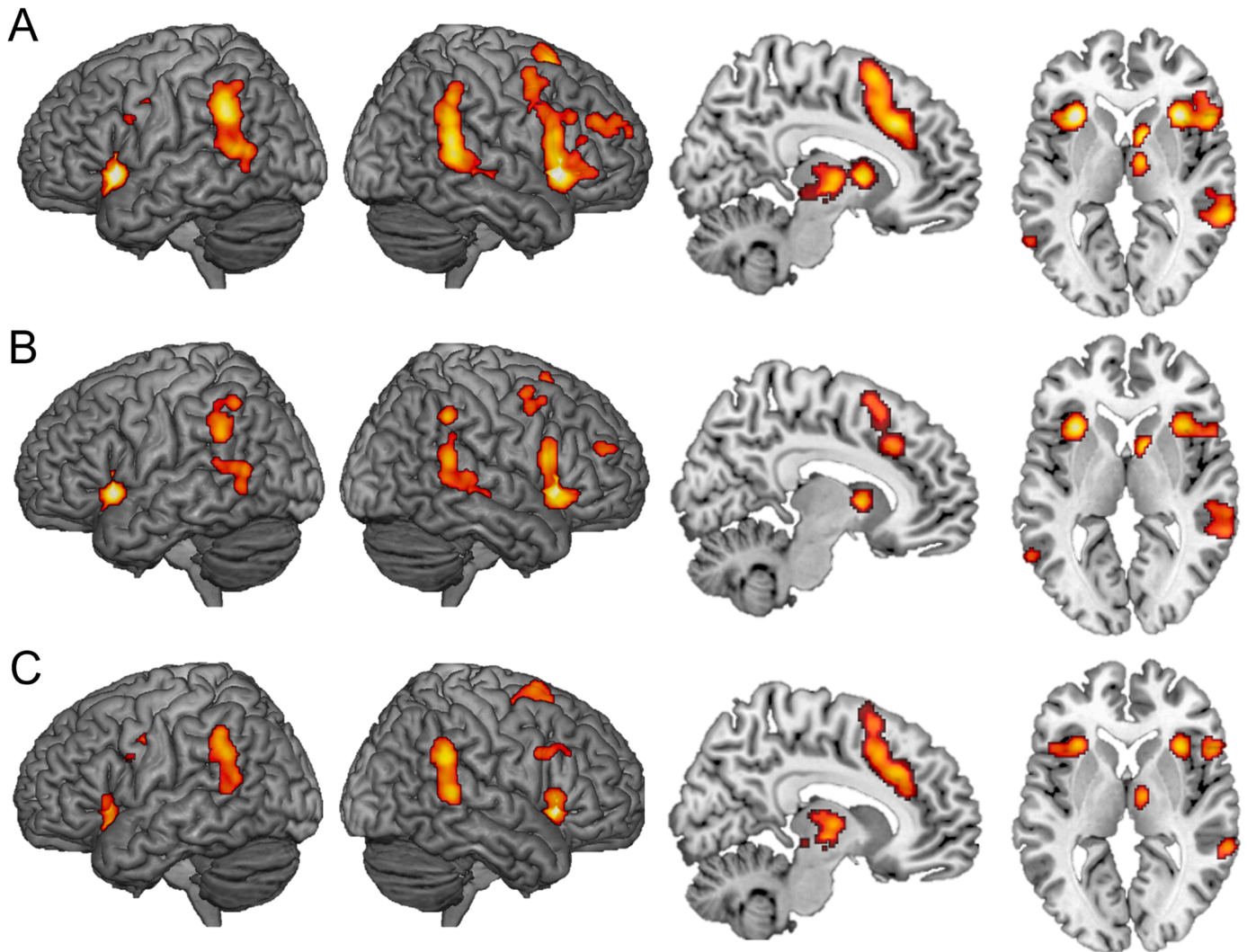


Fig. 3. Meta-analyses across stop-signal task experiments. Brain regions showing significant convergence of brain activity (cluster-level $p < 0.05$ family-wise error-corrected for multiple comparisons, cluster forming threshold $p < 0.001$ at voxel-level) across event-related fMRI experiments including (A) all stop-signal task experiments independent of task complexity, (B) only experiments with standard stop-signal task versions, and (C) only experiments with complex stop-signal task versions.

responses in stop-signal trials, where both – standard and complex – task versions recruited the MDN. In line with behavioral evidence we therefore propose that in classic (standard) GNGT versions, inhibitory control rather quickly becomes automatic after some practice but continues to be implemented in a top-down controlled fashion in the SST (Verbruggen and Logan, 2008a). While the SST thus clearly probes EF processes, this is more questionable for the classic GNGT version (see also Criaud et al., 2013), possibly explaining why performance in one task can deteriorate without an apparent deficit in the other (Krämer et al., 2013; Littman et al., 2017).

4.1. The effect of task complexity on response inhibition

Interestingly, the meta-analysis across the simple GNGT did not reveal convergence in fronto-insular-parietal regions of the classic MDN, with the exception of the right aI and the posterior preSMA/SMA. Besides these two regions, a network consisting of the right IPC, right STS, and bilateral lateral occipital cortex was found. While the finding of mainly lower-level and heteromodal areas outside the classical MDN network being involved in no-go versus go responses in the standard task version may seem to contradict findings from previous meta-analyses (Cieslik et al., 2015; Swick et al., 2011; Puiu et al., 2020; Hung et al.,

2018), it has to be considered that all those earlier meta-analyses did not distinguish between different levels of task complexity. One previous meta-analysis of Simmonds et al. (2008), which included only a very low number of experiments (5 standard, 6 complex experiments), however, also found involvement of higher cognitive areas only for the complex version and thus provided first evidence that the brain network subserving GNGT inhibition strongly depends on the complexity of the paradigm used.

Interestingly, there is behavioral evidence that associations between a stimulus and a no-go response can be established through practice and that these learned associations can be automatically retrieved later on (cf. Verbruggen and Logan, 2008a, Verbruggen et al., 2014, Best et al., 2016; Liefvooghe et al., 2016). Verbruggen and Logan (2008a) for example found that responding was slowed when a go-stimulus had been consistently associated with a no-go-response in a previous training phase, and that response inhibition benefited from consistent stimulus–no-go associations. Hence, the authors concluded that consistent mapping may result in the development of automatic inhibition through the retrieval of established stimulus–no-go associations and that the GNGT may rather probe associative learning than controlled response inhibition. Taking a closer look at the experiments included in the meta-analysis of standard GNGT versions revealed that most designs

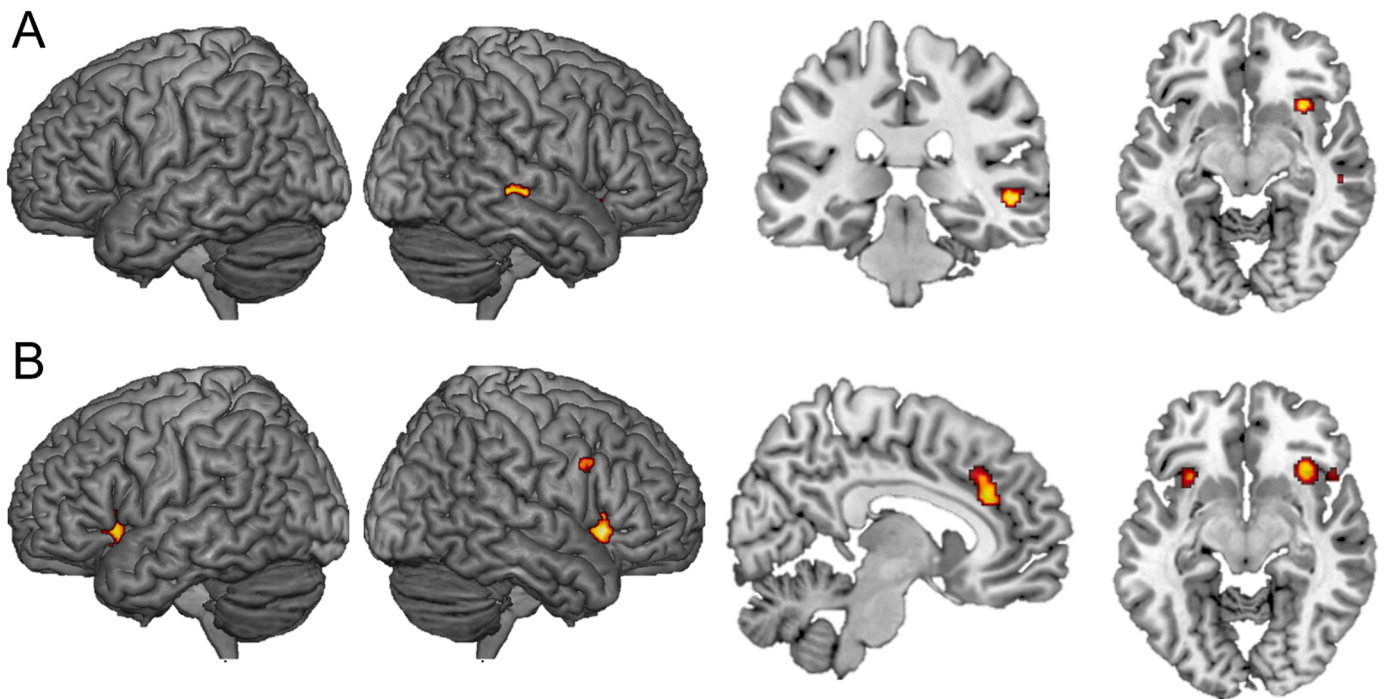


Fig. 4. Conjunction analysis across go/no-go and stop-signal task experiments. (A) Results of the minimum conjunction analysis across the results from the meta-analyses on standard versions of the go/no-go task and stop-signal task respectively, revealing significant conjoint convergence in right anterior insula and right superior temporal sulcus. (B) Results of the minimum conjunction analysis across the results from the meta-analyses on complex versions of the go/no-go task and stop-signal task respectively, revealing significant conjoint convergence in bilateral anterior insula, right inferior frontal junction, and anterior midcingulate cortex.

used one go signal and one no-go signal and thus used a consistent S-R mapping. This allowed participants to learn to react in an automatic manner over time with more practice, and this automatic inhibition may have resulted in reducing the need for top-down executive control. Thus, in combination with these behavioral results, we conclude that in standard GNGT versions with consistent S-R associations, the selection of the go or no-go response is performed in an increasingly automatic manner with practice and, therefore, fewer differences in activity levels between no-go and go trials can be found in brain regions linked to cognitive control.

Further, a recent (electroencephalography) EEG study (Wessel, 2017) using a GNGT version with consistent S-R mapping and varying the stimulus-stimulus interval and the probability of no-go trials, found that only a fast-paced setup with rare no-go trials evoked prepotent motor activity. In the present study, we therefore specifically looked at the probabilities for no-go trials and the stimulus-stimulus intervals as the effect of task complexity may be confounded by trial probability or trial duration (see Table S8b for detailed information on trial probabilities and Table S8b/c for information on trial duration). Overall, there were comparable numbers of standard or complex GNGT experiments using an equiprobable design (five vs. three studies for standard vs. complex GNGT, respectively). Moreover, in the standard GNGT sample, there were three additional studies using varying no-go probabilities, while in the group of complex GNGT versions four experiments included a contrast of rare no-go versus rare go stimuli, in which the probability effect should have been cancelled out. Therefore, we would argue that stronger frontal involvement in complex versus standard go/no-go tasks cannot simply be explained by a trial probability effect. Interestingly, studies comparing no-go versus rare go trials also revealed increased activation in right lateral and inferior PFC (Chikazoe et al., 2009; Fuentes-Claramonte et al., 2016; McNab et al., 2008), even though using equiprobable no-go and rare go trials. Further, we also tested for a difference in mean trial duration between simple and complex GNGT using the Mann-Whitney-U test. Thereby, no significant difference in mean trial duration ($U = 338.5$, $p = 0.21$) was found. In conclusion, it is

unlikely that the stronger frontal convergence observed for complex compared to standard GNGT versions is simply driven by a stimulus probability effect or a difference in trial length. However, future studies should more specifically test for potential interactions between trial probability as well as trial length and task complexity.

In contrast to the GNGT, in the classic SST participants have to cancel an already initiated go response, i.e. reprogram the current action plan, thus requiring top-down control processes. Moreover, in the SST usually a staircase design is used to adapt the stop-signal delay to individual performance, resulting in a 50% success rate for inhibiting the prepotent motor response. Hence, the task is continuously adjusted to individual performance improvements, keeping it sufficiently difficult to ensure continued demand for top-down control in cancellation trials, even in standard task versions. In line with this notion, EEG studies showed reliable inhibition-related activity, in particular the stop-signal P3, for the standard SST (Wessel, 2017; Wessel and Aron, 2015), with the same response inhibition network being recruited in the standard SST and more complex inhibitory control tasks (Wessel and Aron, 2014). The results of our meta-analyses on the SST are in line with those previous findings showing that already the standard SST version consistently recruits key regions of the MDN and that for the complex SST only small variations in the recruitment of MDN regions are found. Thus, it seems that the MDN is already recruited as a whole even in relatively simple versions of tasks effectively probing EF. The finding of rather quantitative variations within the MDN with increasing task complexity or task difficulty is well in line with original fMRI findings indicating that increased task difficulty mainly leads to a different level of involvement within the MDN, rather than to an additional recruitment of more anterior regions in lateral prefrontal cortex (cf. Crittenden and Duncan, 2014).

In conclusion, our meta-analytic results on task complexity in the GNGT and SST indicate that already the standard SST versions recruit the MDN, which can be taken as further indirect evidence that all flavors of the SST probe executive functioning – in particular controlled response inhibition. This, however, is evidently not the case for standard

GNGT versions, which more likely measure automatic response inhibition after some practice and thus do not effectively tax EF-related processing. This also has crucial implications when interpreting behavioral data from patients, as deficits in the GNGT might not reflect difficulties in top-down controlled inhibition but rather difficulties in learning the appropriate S-R contingencies and, therefore, more likely reflect associative learning deficits (cf. Verbruggen and Logan, 2008a). In line with that, it has been shown that schizophrenia patients show deteriorated behavior compared to healthy controls in the GNGT (e.g. Sun et al., 2021; Ertekin et al., 2017; Weisbrod et al., 2000) but also deficits in associative learning (Brambilla et al., 2011; Hall et al., 2009), which might prevent them from learning the correct S-R associations and result in an increased and continued need for top-down control processes over the course of the task.

4.2. Go/no-go and stop-signal tasks: commonalities

4.2.1. Commonalities of standard GNGT and SST versions

The conjunction analysis across the standard task versions revealed conjoint convergence only within the right aI and the right STS. Recruitment of the aI can be observed across a diversity of tasks. In particular, the right aI is thought to play a causal role in activating task-relevant and deactivating task-unrelated regions (Sridharan et al., 2008) and to control activity in other brain regions across different tasks and stimulus modalities to initiate and adjust cognitive control mechanisms (cf. Dosenbach et al., 2006; Sridharan et al., 2008). As a meta-analysis from our group (Cieslik et al., 2015) also found the right aI, together with the right IFJ, to be conjointly involved in Stroop and S-R compatibility tasks as well as GNGT and SST, we would argue that our results further corroborate the notion that the right aI is a key region for monitoring the activation of the relevant task set and sending control signals to other task-relevant regions whenever necessary to enable correct task performance. These processes are evidently not only crucial for very complex cognitive tasks performed in a full-blown top-down mode but also support correct performance in standard tasks, such as the classic GNGT, which increasingly rely on automatic inhibition processes after some practice.

The right STS has less often been discussed in the context of inhibiting a prepotent motor response and is not considered in theories of inhibition (cf. e.g. Stevens et al., 2007; Chambers et al., 2009; Munakata et al., 2011; Wiecki and Frank, 2013). The region within the STS that was found in this meta-analysis most probably corresponds to the mid-STS (Erickson et al., 2017), which has been associated with spoken and written language processing (Wilson et al., 2018) but also with the processing of letters per se (van Atteveldt et al., 2004; Raij et al., 2000). It might thus be speculated that, given that letter stimuli are quite common for GNGT and SST, convergence in mid-STS might reflect processing of those stimuli. A stronger response to no-go and stop stimuli hence might reflect more intense local stimulus processing due to reduced expectancy effects (and thus larger surprise) or higher saliency, as the no-go and stop stimulus are usually presented less often to induce a high response tendency and therefore present a relatively less expected and highly salient stimulus input (cf. Kolodny et al., 2017).

Summarizing, only the right aI and right STS showed common recruitment across both standard task versions, indicating that performance in these two tasks is supported by largely different brain networks, further questioning the practice of pooling results across these two paradigms or using them interchangeably in diagnostic contexts or individual-differences research.

4.2.2. Commonalities of complex GNGT and SST versions

The conjunction analysis across the complex task versions revealed a consistent recruitment of bilateral aI, aMCC, and right IFJ. These regions have been proposed as domain-general regions for supervisory attentional control (cf. Cieslik et al., 2015), mediating controlled activation and maintenance of adequate task schemata necessary to implement

non-routine, goal-oriented behavior.

Like the conjunction across the standard task versions, the investigation across the complex versions revealed convergence in the aI, but with the difference that here convergence was found in both hemispheres. Resting-state functional connectivity (RS-FC) fMRI and task-fMRI studies on functional lateralization suggested that the right aI plays a more general role in attentional control processes and attention reorientation for actions, whereas the left aI has a crucial role in cognitive control important for subsequent behavioral adaptation processes (Kann et al., 2016; Späti et al., 2014). In line with this, our results provide further evidence that the right aI may be more generally involved, with left aI coming into play only when tasks require higher degrees of executive control.

The right IFJ, on the other hand, has been associated with the continuous reactivation of the relevant task rule that links relevant stimulus features and corresponding responses in a task-specific manner (Cieslik et al., 2015). When looking at the contributions of experiments to the right IFJ cluster, we found that primarily tasks with S-R associations that changed depending on context (e.g. GNGT: Garavan et al., 1999; Garavan et al., 2002; Hester et al., 2004a; b; Mander et al., 2010; SST: Lavalley et al., 2014) and the stop-signal anticipation task, where the ever-changing probability of a stop-signal to occur in a given trial is pre-cued (Zandbelt et al., 2010; Zandbelt et al., 2011; Coxon et al., 2016), contributed to convergence in the right IFJ. Hence, consistent involvement of right IFJ in the complex task versions may be explained by the need to continuously update the relevant non-dominant S-R rule (cf. Cieslik et al., 2015), which is particularly needed when stimulus-stop associations change or when stop-signal probabilities are varied across trials.

The other region that was consistently involved in both complex task versions was the aMCC. It has long been argued that the aMCC detects conflict in information processing and concurrently – through interaction with other task-relevant prefrontal areas – leads to adaptation of behavioral action plans according to the current task demand (e.g. MacDonald et al., 2000; see also Botvinick et al., 2004, for a review). Furthermore, aMCC activation has been reported for conditions of free-choice (choice of which hand to use and the specific time point of the movement) where high-level intentional movement control is needed (Hoffstaedter et al., 2013). While the standard SST also consistently recruited the aMCC, involvement across both inhibition tasks was only found for the complex versions. This is well in line with the hypothesis that the aMCC detects conflicting response plans on a higher cognitive level (cf. Cieslik et al., 2015) which arises whenever a prepotent motor plan is in conflict with a task-specific one. This is specifically the case in standard and complex SST when an already initiated motor response has to be canceled. However, as explained above, standard GNGT with consistent S-R mapping may not always elicit a prepotency towards responding (cf. Wessel, 2017) and hence no conflict between concurrent response plans may evolve in the no-go condition, providing a potential explanation for why the aMCC was consistently found only for the complex GNGT.

Besides these three regions, other lateral prefrontal and parietal regions were recruited in a task-specific manner for the complex task versions but did not survive the conjunction analysis. This is well in line with previous data showing that the MDN consists of a core network including bilateral aI, IFJ and posterior medial frontal cortex that together support performance in most EF task, while other parts of the MDN are additionally recruited depending on specific task demands (cf. Camilleri et al., 2018). We here complement these findings by showing that even the complex versions of two tasks designed to tax response inhibition show common recruitment of only the core MDN, with other lateral prefrontal and parietal regions recruited in a more task-specific manner.

4.3. Go/no-go tasks

4.3.1. Standard GNGT versions

Besides the right STS and right aI, which were also found in the conjunction analysis across standard GNGT and standard SST version, bilateral lateral occipital gyrus, right angular gyrus, and a cluster in posterior preSMA, right at the intersection to the SMA, were found to be consistently activated for the standard GNGT version. The bilateral occipital clusters were specifically located in the cytoarchitectonic area hOc41a. A previous study (Malikovic et al., 2016) that functionally decoded this region using the Brainmap database revealed this region to be specifically involved in the processing of shape and orthography. Looking into the contributions in our data, we found that specifically experiments using letters and often infrequent no-go stimuli drove the effect within bilateral hOc41a. This led us to assume that increased convergence for no-go (vs. go) trials in the lateral parts of the occipital cortex may be due to increased visual attention to the specific characteristics of the rare and salient no-go stimuli (cf. also Boehler et al., 2011).

Furthermore, the standard GNGT showed convergence in the angular gyrus, particularly in cytoarchitectonic area PGa (Caspers et al., 2008; Caspers et al., 2006). Interestingly, Wager et al. (2005) revealed specific activation of the right angular gyrus for the GNGT compared to other interference paradigms, such as flanker or S-R compatibility tasks. In accordance with the role of the angular gyrus in the learning, processing, and retrieval of learned schemas and episodic memory (Rugg et al., 2018; van der Linden et al., 2017; Kuhl et al., 2014), convergence in PGa for the GNGT might hence reflect recruitment of learned automatic memory-based S-R representations (e.g. X = no-go and O = go).

The preSMA/SMA, on the other hand, has been associated with selecting the appropriate motor response from different alternatives (for a review, see Nachev et al., 2008) and is strongly related to tasks requiring cognitive control of motor responses, such as task switching or word generation (Eickhoff et al., 2011). In comparison to the higher-level preSMA, the SMA is thought to be more directly related to generating motor output, especially to action execution processes in relatively simple paradigms such as finger tapping, saccades or imagined movements (Nachev et al., 2008). Previous investigations that distinguished between standard and complex GNGT also revealed a crucial role for the posterior preSMA/ SMA for response selection processes in standard task versions (Mostofsky et al., 2003; Mostofsky and Simmonds, 2008; Simmonds et al., 2008). Thus, given previous results of its involvement in motor selection in relatively simple tasks, we suggest that the convergence we observed in posterior preSMA/ SMA reflects response selection processes that can be performed in a relatively automatic manner in the standard GNGT version.

In summary, a neural network outside the classical MDN network was found to be consistently involved in the standard GNGT. This finding may be somewhat surprising at first sight but most likely reflects the fact that responding in standard GNGT versions may become more automatic with practice, hence reducing the need for higher cognitive control regions usually found in other tasks probing inhibitory control or EFs in general.

4.3.2. Complex GNGT versions

In contrast to standard GNGT versions, more complex versions of the paradigm were consistently associated with the classic MDN. That is, besides the three supervisory attentional control regions that showed common involvement in the complex GNGT and SST (cf. 4.2.2), additional convergence was found in the parietal cortex, two regions of the right DLPFC, and rIFG. Moreover, subcortical convergence was found in bilateral anterior putamen.

While recruitment of the right DLPFC is frequently reported in studies investigating response inhibition, its role remains controversial (cf. e.g. Criaud et al., 2013). It has been suggested that the DLPFC is involved in rule-based selection of responses with a fundamental role in

linking memory representations to goal directed motor behavior (c.f. Ridderinkhof et al., 2004). In line with this notion a lot of experiments that contributed to convergence within the mid-DLPFC exhibited increased WM demands, that is, when the no-go response was defined by a rule referring to preceding events, such that participants had to withhold their responses when the order of an alternating stimulus presentation was broken (e.g. Garavan et al., 1999, 2003; Hester et al., 2004a; b). Thus, participants could not learn a specific S-R association but had to activate the no-go response depending on a rule and a trial-by-trial adjustment if the current stimulus differed from the one presented before.

Little is known about the role of the anterior portion of the DLPFC in tasks requiring conflict monitoring and response selection (cf. Badre and Wagner, 2004). Previous studies have proposed a hierarchical organization within the LPFC, with the frontopolar cortex implementing the highest level of executive control, involving evaluation of information that has been generated at lower levels of executive processing within the DLPFC (cf. Christoff and Gabrieli, 2000). Looking at the contributions, we see that especially task variants with an oddball component or an additional interfering stimulus component (such as the word “PRESS” in red colors used as the no-go stimulus) contributed to the aDLPFC cluster. These variants may exacerbate the selection of the correct response and hence result in the activation of more anterior prefrontal areas in order to select the right response to a specific stimulus in more complex task conditions. This is most likely performed together with the parietal cortex (particularly IPS and SPL), which plays a crucial role in the integration of visuo-spatial, motor, and memory information into S-R associations under the control of the DLPFC (Corbetta and Shulman, 2002; Gottlieb, 2007), and which showed consistent involvement in the present study but also previous meta-analyses of GNGT-related brain activity (Cieslik et al., 2015; Simmonds et al., 2008; Swick et al., 2011).

Furthermore, we also found convergence in the right IFG, which was also found for the standard SST, but not the standard GNGT. As mentioned in the introduction and further discussed in Section 4.4.1. the right IFG is commonly discussed as the key region of controlled response inhibition. The lack of convergence of the right IFG in the standard version of the GNGT could be attributed to a lack of top-down control needed in these task versions. Increased task difficulty due to e.g. complex stimuli or higher working memory load in the complex GNGT version may contribute to a higher cognitive effort, resulting in involvement of the right IFG.

Subcortically, the complex GNGT revealed consistent activity in bilateral anterior putamen. Previous fMRI studies suggest that the putamen plays a critical role in the prediction of stimuli or targets especially in uncertain situations and thus also reflect predictions errors, which may result in the optimization and learning of the S-R association involved in the response selection process (Ouden et al., 2009; Sommer et al., 2016). In line with this, investigation of the influence of antagonists on dopamine receptors in the putamen of monkeys showed that dopamine receptors play a critical role in response selection (Ueda et al., 2017). The putamen may hence play a pivotal role for selecting the correct response in the complex GNGT as increased task difficulty results in higher risk for a prediction error and thus additional control is needed.

In conclusion, we have shown that the neural network commonly associated with action withholding in the GNGT crucially depends on stimulus complexity and particular design features of the variant used. Hence, activity in lateral prefrontal and superior/ intra-parietal regions more likely reflect higher executive processes that come into play whenever the task cannot be performed in an automatic manner and increased executive control mechanisms are needed to enable correct task performance.

4.4. Stop-signal tasks

4.4.1. Standard SST versions

In addition to convergence in the STS and right aI, that were already discussed in [Section 4.2.1](#), the meta-analysis across standard SST versions revealed significant convergence in left IPC, right IPS, bilateral TPJ and STS, aMCC/preSMA, right dPMC, bilateral aI extending into IFG particularly in the right hemisphere, right IFJ, and right DLPFC. Moreover, subcortical convergence was found in right caudate nucleus.

Neural models of response inhibition classically include cortical regions, in particular the IFG and preSMA, that project to the globus pallidus pars interna/externa via either the striatum or the subthalamic nucleus (STN) and then back to the cortex via the thalamus (see [Jahfari et al., 2011](#); [Aron et al., 2007a](#); [Aron, 2007b](#)). It has been argued that within this network the right IFG plays a crucial role for the cancellation of the prepotent motor plan, with greater activity during stopping in right IFG and STN in participants with quicker stop-signal reaction times (i.e., in people showing more efficient inhibitory control; [Aron and Poldrack et al., 2006](#)). However, the specific functional role of this region is still a matter of debate. In particular, TMS over right IFG not only leads to disturbed SST performance ([Chambers et al., 2007](#)) but also increased dual-task costs, providing evidence that the right posterior IFG may implement control processes by updating actions plans according to changes in behaviorally relevant stimuli ([Verbruggen et al., 2010](#)). Supporting this view, a recent comparison of human fMRI and electrophysiological findings in primates in a context-dependent SST proposed that the ventral part of the IFG, comparable to our rIFG convergence cluster, is responsible for registering the intention to stop, or updating the current action plan, given the present context and stimulus ([Xu et al., 2017](#)). Concluding, the right IFG most likely supports reactive inhibitory control by updating action plans after presentation of the stop-signal.

Interestingly, the DLPFC cluster showing convergence for the SST was localized between the two DLPFC cluster showing convergent activity for the complex GNGT. It hence seems to play a specific role in the context of SST performance. This DLPFC cluster overlapped with an anterior DLPFC cluster defined by a previous co-activation based parcellation study that revealed specific connectivity with the anterior cingulate cortex ([Cieslik et al., 2013](#)). Moreover, the study argued that this region is involved in the monitoring of motor responses and subsequent behavioral adjustments, if necessary. As the SST requires to cancel the already initiated go-response once the stop-stimulus is identified, we argue that the DLPFC cluster that showed consistent increased activity for stop versus go responses in our meta-analysis may be involved in mediating the required behavioral adjustment processes.

The other region within the frontal cortex that was consistently recruited in the standard SST versions was the right dPMC. The dPMC is a key region for movement planning and execution ([Nakayama et al., 2016](#); [Cisek et al., 2005](#)), but has frequently also been associated with inhibition processes during reaching movements in investigations of the SST in primates ([Mirabella et al., 2011](#); [Giarrocca et al., 2021](#)). In line with this, TMS-induced disturbance of the dPMC resulted in a significant rise of errors in stop trials ([Parmigiani and Cattaneo, 2018](#)). Strong connectivity between the dPMC and motor areas ([Koch et al., 2006](#); [Nakayama et al., 2016](#)) and evidence from TMS studies showing that the dPMC exerts control over the primary motor cortex ([Bestmann et al., 2008](#); [Parmigiani et al., 2015](#)) lead us to conclude that the dPMC plays a key role for the stopping of initiated motor plans more at the output level, through its direct inhibitory influence on primary motor areas.

Within the medial frontal cortex, the preSMA has been associated with successful inhibition of motor responses (cf. [Sharp et al., 2010](#)) and hypothesized to closely interact with the IFG during SST performance ([Swann et al., 2012](#)). The preSMA most likely exerts an active role in the selection between different response alternatives (see above). Dynamic causal modeling analyses have suggested that the preSMA resolves competition between concurrent motor plans by exerting inhibitory and excitatory executive control over the motor cortices ([Cieslik et al.,](#)

[2011](#)). Interestingly, the cluster showing convergence for standard SST versions lay anterior to the posterior preSMA/SMA region that was found for standard GNGT versions, providing further evidence for a functional gradient along the rostral-caudal axis, with more anterior regions being involved in cognitively more demanding control processes for selecting the correct response alternative. In contrast, response selection processes relying on automatic inhibition, as presumably occurring in standard GNGT versions, are subserved by more posterior regions.

Standard SST versions furthermore showed convergent activity in the TPJ, a central region in the ventral attentional control network involved in reorienting attention to task-relevant, currently unattended, stimuli ([Corbetta et al., 2008](#)). It was furthermore suggested that the TPJ takes part in the contextual updating of behavior in order to choose appropriate actions in regard to changing environmental inputs ([Geng and Vossel, 2013](#)). Both attention reorientation and contextual updating are crucial for correct performance in the SST suggesting that the TPJ is associated with attention orientation to the stop-stimulus, signaling participants to update the current action plan such that the action program is canceled.

Subcortically, significant convergence of activity was found within the caudate nucleus. The caudate is part of the indirect pathway of the basal ganglia circuit and proposed to be particularly involved in proactive inhibition ([Jahfari et al., 2011](#); [Zhang and Iwaki, 2019](#)). However, we here found consistent stronger activity for stop versus go trials, providing evidence that the caudate nucleus is also involved in reactive inhibition, when the stop-signal is presented. fMRI evidence argues for a direct link between caudate activity and behavioral performance. For example, a study in ADHD patients showed that decreased activity in the right caudate for successful versus unsuccessful stopping goes along with decreased behavioral performance in the SST ([Sebastian et al., 2012](#)). Further, a recent fMRI study showed that activation within bilateral caudate nucleus covaries with a parameter of selective inhibition derived during the Simon task, pointing to a crucial role of the caudate for the selective inhibition of interfering response tendencies ([Schmidt et al., 2020](#)). Concluding, consistently stronger activated for stop versus go trials within the caudate nucleus may reflect increased need for selective inhibition.

4.4.2. Complex version

As shown in [Fig. 3](#), standard and complex SST versions showed convergence in very similar brain regions - with some variation in the exact location and extent of significant clusters, particularly in the lateral frontal cortex. Moreover, compared to the standard version the complex SST additionally recruited the thalamus and IFJ on the left side.

While involvement of the right IFJ, which was also found for the conjunction analysis of the complex GNGT and SST versions, can be attributed to continuous updating of the relevant but non-dominant S-R rule (see [Section 4.2.2.](#)), convergence in the left IFJ might reflect additional activity to support this process in more difficult conditions. That is, left IFJ has commonly been reported in task-switching paradigms ([Kim et al., 2012](#); [Worringer et al., 2019](#)) that require participants to constantly update and switch the currently relevant task set. In line with this notion, left lateral PFC, including IFJ, has specifically been found during the implementation of novel task rules ([Hartstra et al., 2011](#); [Hartstra et al., 2012](#)). [Ruge and Wolfensteller \(2010\)](#) found BOLD signal activity present specifically in the first trials of newly instructed S-R mappings, while its activation level decreased with increasing practice. This effect is well in line with evidence from patients with left lateral PFC lesions, who revealed deficits particularly in the initial stages of learning new tasks (when new task schemas had to be acquired) but showed performance comparable to healthy controls in later trials ([Shallice et al., 2008a,b](#)). Additional recruitment of the left IFJ in complex SST versions may hence be explained by the more difficult implementation of S-R associations in more complex task versions.

The thalamus is frequently reported to be part of a frontal-striatal-

thalamic network recruited during stopping of actions (Aron and Poldrack, 2006; Aron, 2011; Congdon et al., 2010; Wilbertz et al., 2014; Hughes et al., 2014; Bellgrove et al., 2004). Comparing our thalamic cluster with parcellations of the thalamus based on structural connectivity (Behrens et al., 2003) and RSFC data (Zhang and Li, 2017) shows that the part of the thalamus showing convergence in our meta-analysis is connected with the prefrontal cortex. Interestingly, the thalamus seems to be specifically involved in the cancellation of actions rather than action withholding (Dambacher et al., 2014; Swick et al., 2011), which is in line with our finding of convergence during complex SST but not GNGT versions. Furthermore, a recent study showed that activation of a frontal-striatal-thalamic circuit correlated negatively with stop-signal reaction time in healthy adults, whereas this was not the case in patients with cocaine addiction, who showed a general slowing (Wang et al., 2018). We hence here provide further evidence that the thalamus, together with the prefrontal cortex, forms a neural circuit recruited when an already initiated motor response has to be canceled.

5. Limitations

There are some limitations of the present study, we would like to discuss.

Unfortunately, our complex category included very different versions of the GNGT and SST, respectively, which differed, for instance, in the perceptual complexity of the stimulus, the selectivity of inhibition, or the involvement of other cognitive processes. It would be interesting to investigate the impact of these different types of complexity. However, for performing robust and valid ALE meta-analyses, a minimum number of 17 to 20 experiments is needed (Eickhoff et al., 2016). As the complex GNGT category included 27 experiments, and the complex SST included 25 experiments, we were not able to perform any sub-analysis focusing on different complexity levels. Interestingly, while there is some literature on the effects of increased task difficulty on the MDN (e.g. Crittenden and Duncan, 2014; Shashidhara et al., 2019), increasing stimulus complexity may sometimes even lead to a reduced involvement of the MDN (cf. Smith et al., 2021). When looking at the contributions of individual experiments to clusters of convergence, we found that experiments featuring increased stimulus complexity particularly contributed to convergence within the IPS, providing further evidence for a specific role of the IPS in the identification and selection of relevant stimulus features for response selection. However, this hypothesis needs to be formally tested and future studies need to further disentangle the specific contribution of, e.g., stimulus versus task complexity on the different regions within the MDN.

Moreover, ALE meta-analyses test for consistency of spatially located effects without considering information on activation strength (i.e., effect size; cf. Müller et al., 2018). Thus, we cannot say exactly how activity is modulated when task difficulty is increased in a stepwise fashion. For instance, evidence from the WM literature points toward differential responding of lateral PFC to increasing WM load, with activity increases with increasing WM load but a reversal of this effect once WM load exceeds a critical level (e.g. van Snellenberg et al., 2015; Linden et al., 2003; Ahmed and Fockert, 2012). Hence, future studies should not only compare two different complexity levels per task but use different modulations of task complexity to better understand the specific neural response of key regions in the MDN.

Furthermore, when looking at potential hemispheric asymmetries in the SST it seems that especially in lateral prefrontal cortex some stronger involvement of the right hemisphere can be observed. As the information of activation strength is lost in ALE meta-analyses, we cannot provide any direct evidence for a differential engagement of the two hemispheres. However, it seems that for the lateral PFC, especially the right side is consistently recruited in the SST, while insular, middle frontal cortex, and temporo-parietal regions are recruited more bilaterally.

Lastly, a comprehensive understanding of the commonalities and

differences between the GNGT and SST will not only require results from pooled data across participants, but also calls for investigating the two tasks within the same participants, to account for inter-individual variance when comparing activation patterns. A recent ultra-high field fMRI study compared response inhibition with interference resolution using the SST and a multi-source interference task, respectively (Isherwood et al., 2023). Using a model-based approach they found that behavior in the two tasks relied on distinct brain regions, with little spatial overlap. Further, as there was no strong correlation between modeling parameter estimations, the authors concluded that the two processes are also largely independent on the behavioral level. Thus, future fMRI studies should consider model-based approaches to achieve a more precise representation of the differences between tasks on the behavioral as well as the neural level (cf. Sebastian et al., 2018).

6. Conclusion

While results from the GNGT and SST have often been pooled together when delineating the neural correlates of inhibitory control, we found a divergent set of regions involved in standard GNGT versus SST, suggesting different underlying mechanisms. Task complexity strongly affected the pattern of regions involved in withholding responses in no-go trials, with the MDN coming into play particularly in the complex GNGT versions. We thus argue that the standard GNGT version can be performed in a rather automatic manner once S-R contingencies have been learned. In contrast, both standard and complex SST recruited a very similar set of regions, indicating that increasing task complexity results in quantitative (rather than qualitative) variations within the MDN in tasks which effectively probe EF. Furthermore, the conjunction analysis across the complex task versions revealed common involvement of only bilateral aI, aMCC and right IFJ, regions that have been proposed to mediate supervisory attentional control processes (Cieslik et al., 2015). Other regions of the MDN, such as lateral prefrontal or parietal cortex, hence seem to be less domain-general but recruited depending on specific task demands.

Concluding, we argue that the GNGT and SST test different concepts of inhibition – automatic versus controlled inhibition – and should not be treated interchangeably.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neubiorev.2024.105544.

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