



Review

Three key regions for supervisory attentional control: Evidence from neuroimaging meta-analyses



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ABSTRACT

The supervisory attentional system has been proposed to mediate non-routine, goal-oriented behaviour by guiding the selection and maintenance of the goal-relevant task schema. Here, we aimed to delineate the brain regions that mediate these high-level control processes via neuroimaging meta-analysis. In particular, we investigated the core neural correlates of a wide range of tasks requiring supervisory control for the suppression of a routine action in favour of another, non-routine one. Our sample comprised $n = 173$ experiments employing go/no-go, stop-signal, Stroop or spatial interference tasks. Consistent convergence across all four paradigm classes was restricted to right anterior insula and inferior frontal junction, with anterior midcingulate cortex and pre-supplementary motor area being consistently involved in all but the go/no-go task. Taken together with lesion studies in patients, our findings suggest that the controlled activation and maintenance of adequate task schemata relies, across paradigms, on a right-dominant midcingulo-insular-inferior frontal core network. This also implies that the role of other prefrontal and parietal regions may be less domain-general than previously thought.

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1. Introduction

Flexible, adaptive behaviour requires continuous balancing between the initiation and inhibition of actions, such as when a prepotent response has to be suppressed in favour of a contextually appropriate one. Cognitive control of action is particularly important in the presence of a changing environment or the up-dating of goals and intentions (cf. [Boehler et al., 2010](#); [Schachar et al., 2007](#); [Miller and Cohen, 2001](#)). [Norman and Shallice \(1986\)](#) developed a theoretical framework for the implementation of goal-directed, non-routine behaviour against competing pre-dominant, routine responding. According to this framework, automatic or routine actions are based on the activation and implementation of a task schema that represents a learned sequence of input–output rules. Schemata can be activated by triggers, such as sensory input or the outcome of other schemata ([Stuss et al., 1995](#)). During well-learned routine behaviours, competition between schemata is controlled by lateral inhibition mechanisms, termed “contention scheduling.” However, the coordination of schemata with higher-level, overarching goals requires the additional employment of a “supervisory attentional system” (SAS), which exerts top-down control by deactivating certain schemata and activating others in the service of higher-order goals (cf. [Alexander and Brown, 2010](#)). The implementation of non-routine behaviour against predominant but inadequate response tendencies specifically relies on different sub-processes of the SAS that have been anatomically localized in the frontal cortex. In particular, lesion studies revealed a crucial role of the dorsomedial frontal cortex for energization, the process of initiating and sustaining the currently relevant task schema (cf. [Stuss and Alexander, 2007](#)). This sub-process would become necessary whenever a task schema needs to be activated that is not triggered automatically by perceptual and motivational input (cf. [Shallice et al., 2008b](#)). In contrast, patients with lesions in the left lateral prefrontal cortex (PFC) show deficits in task-setting, which sets the specific stimulus–response contingencies and is specifically required in the initial stages of learning a task ([Shallice et al., 2008a, 2008b](#)). Right lateral PFC, on the other hand, has been associated with monitoring processes, such as continuously checking the appropriateness of the behavioural output ([Stuss, 2006, 2011](#)).

Frequently used tasks that require participants to suppress a predominant response in favour of an appropriate, context-dependent one comprise the Stroop, flanker, Simon, stimulus–response compatibility (SRC), and antisaccade tasks as well as stop-signal and go/no-go tasks (cf. [Diamond, 2013](#); [Nee et al., 2007](#); [Sebastian et al., 2013](#)). All these tasks have very often been conceptualized as paradigms that tax inhibitory action control. Poor performance in these tasks has hence been commonly explained as a prefrontally mediated deficit in inhibiting the inappropriate response. However, recent evidence points to a more general role of the PFC in these tasks, being crucial for the active maintenance of task goals as well as the activation of the appropriate behavioural alternative ([Everling and Johnston, 2013](#); [Munakata et al., 2011](#)).

In the present study, we aimed at isolating and functionally characterizing brain regions that are essential for the coordination between the inhibition of a predominant, inappropriate response and the activation of the goal-dependent one. We used coordinate-based activation likelihood estimation (ALE) meta-analyses ([Eickhoff et al., 2009, 2012](#); [Turkeltaub et al., 2002, 2012](#))

to integrate results from a diverse range of neuroimaging studies investigating the stop-signal, go/no-go, Stroop, flanker, SRC, antisaccade, and Simon tasks. All of these paradigms require cognitive control over a predominant response tendency and the context-dependent initiation of an appropriate behavioural alternative, that is, either to initiate an alternative, non-dominant response or not respond at all.

In go/no-go and stop-signal tasks, an increased automatic tendency to initiate a particular motor response is induced through a higher frequency of go trials, as compared with inhibition (i.e. no-go or stop) trials. The resulting action bias then has to be suppressed when presented with the inhibition signal during stop or no-go trials, respectively. While in the go/no-go task participants have to withhold a prepotent but not-yet initiated motor response, the stop-signal task requires cancelling an already initiated motor response (cf. [Eagle et al., 2008](#); [Schachar et al., 2007](#)). In the other tasks, which can be subsumed under the term “incongruency tasks”, a given stimulus dimension interferes with relevant stimulus and/or response information, thereby affecting responses to the relevant information. According to the dimensional overlap model ([Kornblum et al., 1990](#); [Kornblum and Stevens, 2002](#)), overlap between a (irrelevant) stimulus dimension and the response dimension results in an automatic translation of the stimulus feature into a response code. During congruent trials, the automatically activated response and the required one are one and the same. In contrast, during incongruent trials, the required response differs from the automatically activated one, thereby leading to an incongruency effect reflected in increased reaction times and error rates. Interestingly, it has been shown that the use of spatial as opposed to non-spatial information may lead to larger (in-)congruency effects in the context of some tasks. For example, [Zeischka et al. \(2010\)](#) investigated the congruency effect in different versions of the flanker task and found increased congruency effects when using arrows as stimuli, as compared to letters or colours. One possible explanation for this finding may be that the use of spatial information produces a simultaneous shift in both (perceptual) spatial attention and (motor) response activation on the ipsilateral side ([Cieslik et al., 2010](#); [Notebaert et al., 2001](#); [Stoffer and Yakin, 1994](#)).

Summarizing, we investigated four subcategories of cognitive action control. Action withholding was assessed with the go/no-go task that requires participants to withhold a prepotent but not yet initiated motor response. In contrast, the stop signal task investigates inhibition of an already initiated motor response, which can hence be conceptualized as action cancellation (cf. [Eagle et al., 2008](#); [Schachar et al., 2007](#)). Interference control, finally, was investigated by means of congruency tasks that require participants to solve interference between competing response plans, by inhibiting the prepotent response and concurrently initiating the context-appropriate one. The latter were further subdivided into (non-spatial) Stroop versus spatial interference tasks (comprising Simon, SRC, antisaccade and spatial flanker tasks).

In a first step, we tested which brain regions are consistently associated with the four paradigm classes, that is, go/no-go, stop-signal, Stroop and spatial interference tasks. In a second step, we aimed to reveal those regions that are consistently activated whenever the task context requires inhibiting the predominant response and concurrently activating the appropriate task goal for initiating the adequate behaviour. We therefore performed a conjunction analysis across the thresholded ALE maps of all four task types. As

all these four paradigm classes require (i) the suppression of actions that are inappropriate in a given context (ii) and the concurrent initiation of the context-appropriate behaviour, this approach should reveal those regions that are critical for the regulatory processes mediated by the SAS.

2. Methods

2.1. Paradigms included:

For our meta-analysis, neuroimaging results on the neural correlates of seven different tasks investigating cognitive control of actions were included, namely the Stroop, flanker, Simon, SRC, antisaccade, go/no-go and stop-signal tasks.

Stroop task: In the (standard) colour-word Stroop task (Stroop, 1935), participants are required to suppress a prepotent response, the reading of a word, in favour of a less dominant one, the naming of the ink colour in which the word is written. There are three possible types of trials: (i) congruent trials, in which the colour of the word matches the word's referent (e.g., the word "red" printed in red); (ii) incongruent trials, in which ink colour and word differ (e.g., the word "blue" printed in red); and (iii) neutral trials, in which the colour of the word and the word's referent do not provide competing responses (e.g., a series of "X"s printed in red). Other, less common variants such as the numerical Stroop task, where participants have to identify which of two presented numbers is written in a higher font size while ignoring the numerical size, were included as well. In contrast, emotional versions of the Stroop task were not included as there is evidence from behavioural and neuroimaging studies that interference arising from emotional distractors may rely on different processes and neural correlates than interference from non-emotional ones (e.g. Egner et al., 2008; Frings et al., 2010; McKenna and Sharma, 2004).

Flanker task: In the flanker task (Eriksen and Eriksen, 1974), participants are asked to identify and respond to a central target stimulus, such as a letter or an arrow, and to ignore similar distractor stimuli flanking the target. Participants show longer reaction times when the flankers are associated with a different response than the target stimulus (incompatible trial), as compared with trials in which the flankers and the target are associated with the same response (compatible trials) (Eriksen and Eriksen, 1974; Miller, 1991).

Simon task: In the Simon task (Simon, 1990), participants have to respond to a non-spatial stimulus dimension according to an arbitrary rule while ignoring the spatial dimension of the stimulus. Typically, variously coloured stimuli are matched with different responses (say, blue: left-hand response, yellow: right-hand response). When the blue stimulus is presented in the right hemifield (incongruent condition), the irrelevant (but, due to over-learned spatial S-R associations, still influential) spatial placement of the stimulus automatically activates right-hand response codes and interferes with the actually required (i.e., left-hand) response. This, in turn, leads to increased reaction times and error rates, as compared with a spatially congruent condition.

Antisaccade task: In the antisaccade task (Hallett, 1978), participants are instructed to fixate a central position and, after the presentation of a lateralized target stimulus, to perform a saccadic eye-movement (antisaccade) to its mirror-symmetrical position. Participants usually show increased reaction times and error rate when instructed to perform an antisaccade compared to a prosaccade (eye-movement to the lateralized target).

SRC task: Here, participants are required to respond to a stimulus according to its spatial dimension, with the spatial S-R mapping being either compatible or incompatible. A typical example for a congruent mapping would be a left-sided motor response to

a left-pointing arrow or a left-lateralized stimulus, while in the incongruent condition, participants would have to respond to these stimuli with their right hand. Incongruent S-R mappings lead to an increase in reaction time and error rate (Fitts and Seeger, 1953).

Go/no-go task: The traditional go/no-go paradigm usually involves two different stimuli, a "go" and a "no-go" stimulus, that are presented in a random sequence. Participants are instructed to rapidly respond to go stimuli, while withholding the response to no-go stimuli. The prepotency towards responding, rather than withholding, is usually achieved by having more go than no-go stimuli in a given block of trials.

Stop-signal task: Here, participants are required to make speeded choice reactions to different target stimuli such as letters. On some trials, a second (e.g. auditory) stimulus is presented shortly after the target, instructing participants to cancel their (often already initiated) response (Logan et al., 1997).

2.2. Selection criteria for the experiments included in the meta-analyses

Relevant neuroimaging experiments for the meta-analyses were obtained from literature search in PubMed (www.pubmed.com) as well as reference tracing in these retrieved papers and in review articles. Only results from whole-brain group analyses reported as coordinates in a standard reference space (Talairach/Tournoux or Montreal Neurological Institute (MNI)) were included, while results of region-of-interest (ROI) analyses were excluded. Furthermore, only data from healthy adults were included, while data from children and patients were excluded. When patient studies separately reported results from a healthy control group, the results from the healthy group were included. Data from conditions with pharmacological or non-invasive manipulations such as Transcranial Magnetic Stimulation were excluded even if they reported a control group receiving only a placebo condition due to possible anticipation effects that might influence behavioural output as well as underlying neural responses. Moreover, single-subject reports as well as experiments investigating between-group effects pertaining, for example, to handedness, sex, or genotype were excluded. In the present meta-analyses, only contrasts reporting neural correlates of increased demands on cognitive action control contrasted with an "active" control condition were included. Experimental effects compared with a resting baseline and reverse contrasts (i.e. "deactivations"), which are much less consistently reported in the literature, were not considered. Consequently, in the stop-signal and go/no-go task, the critical contrast was inhibition vs. go. However, some go/no-go experiments did not model go trials as separate regressors but included them in the baseline; these experiments were also included as we considered the "baseline" in these experiments an active control condition. In all other tasks, the critical contrast was incongruent vs. congruent, with the Stroop, Simon and flanker tasks also including some experiments contrasting incongruent with neutral conditions (see Table S1).

Based on these criteria, 62 experiments investigating the Stroop task, 32 experiments investigating the go/no-go task, 24 experiments investigating the stop signal task, 19 experiments investigating the flanker task (with 11 of these using arrows as stimuli), 15 experiments investigating the Simon task, 11 experiments investigating the SRC task, and 10 experiments investigating the antisaccade task were identified as eligible for inclusion in the meta-analysis. The Simon, flanker (only those 11 using arrows as stimuli), SRC and antisaccade experiments were subsumed under the category "spatial interference task," given the relatively low number of available experiments for these tasks and, in particular, their common focus on spatially based conflict (cf. Zeischka et al., 2010). To ensure that the results in this mixed group of

spatial conflict tasks was not driven by any particular paradigm type, the number of experiments was matched by randomly selecting 10 experiments of every paradigm class. Differences in coordinate space (MNI vs. Talairach space) were accounted for by transforming coordinates reported in Talairach space into MNI coordinates using a linear transformation (Lancaster et al., 2007).

In summary, we investigated four different instances of cognitive action control: (1) action withholding as assessed by the go/no-go task ($n = 32$), (2) action cancellation as assessed by the stop signal task ($n = 24$), and (3 and 4) two forms of interference control, as assessed by the Stroop task ($n = 62$) and by spatial conflict task ($n = 40$), respectively. Furthermore, minimum conjunction analyses were performed as the key objective of the present study was to isolate those regions that consistently mediate the coordination between the inhibition of a predominant, inappropriate response and the activation of the goal-dependent, behavioural alternative across different task contexts.

2.3. Activation likelihood estimation algorithm

All meta-analyses were performed using the revised ALE algorithm for coordinate-based meta-analysis of neuroimaging results (Eickhoff et al., 2009, 2012; Laird et al., 2009a, 2009b; Turkeltaub et al., 2002) according to the standard procedures of our institute (cf. Langner and Eickhoff, 2013; Rottschy et al., 2012). This algorithm aims to identify areas showing a convergence of reported coordinates across experiments that is higher than expected under the assumption of random spatial associations. The key idea behind ALE is to treat the reported foci not as single points but rather as centres for 3-D Gaussian probability distributions capturing the spatial uncertainty associated with each focus. The width of these uncertainty functions was determined based on empirical data on the between-subject and between-template variance, which represent the main components of this uncertainty. Importantly, the applied algorithm weights the between-subject variance by the number of examined subjects per study, accommodating the notion that 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 probabilities of all foci reported in a given experiment were then combined for each voxel, resulting in a modelled activation (MA) map (Turkeltaub et al., 2012). Taking the union across these MA maps yielded voxel-wise ALE scores describing the convergence of results across experiments at each particular location of the brain. To distinguish ‘true’ convergence across studies from random convergence (i.e., noise), ALE scores were compared to an empirical null-distribution reflecting a random spatial association between experiments. Hereby, a random-effects inference is invoked, focussing on inference on the above-chance convergence across studies, not clustering of foci within a particular study. Computationally, deriving this null-hypothesis involved sampling

a voxel at random from each of the MA maps and taking the union of these values in the same manner as done for the (spatially contingent) voxels in the true analysis, a process which can be solved analytically (Eickhoff et al., 2012). The p -value of the ‘true’ ALE 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 then thresholded at a cluster-level corrected threshold of $p < 0.05$ (cluster-forming threshold at voxel level: $p < 0.001$, uncorrected) and transformed into z -scores for display. Conjunction analyses were performed by using the conservative minimum statistic (Nichols et al., 2005) to identify voxels where a significant effect was present in all separate analyses.

All results were anatomically labelled by reference to probabilistic cytoarchitectonic maps of the human brain using the SPM Anatomy Toolbox (Eickhoff et al., 2005, 2007). Details on these cytoarchitectonic regions may be found in the following publications on Broca’s region (Amunts et al., 1999), inferior parietal cortex (Caspers et al., 2006, 2008), superior parietal cortex and intraparietal sulcus (Choi et al., 2006; Scheperjans et al., 2008a, 2008b), motor cortex (Geyer et al., 1996), and the thalamus (connectivity-based regions; Behrens et al., 2003).

3. Results

3.1. Meta-analysis of all included experiments

In a first step, we identified those brain regions that showed significant convergence across all 173 experiments. This main-effect revealed consistently increased activity in a bilateral frontoparietal network, consisting of anterior insula (aI) and adjacent inferior frontal gyrus (IFG), dorsolateral prefrontal cortex (DLPFC), dorsal premotor cortex (dPMC), as well as bilateral intraparietal sulcus (IPS) extending into superior parietal lobe (SPL). Moreover, convergent activity was found in the right temporoparietal junction (TPJ) and in the left inferior occipital gyrus as well as in the (pre)-supplementary motor area [(pre)SMA] extending into the anterior midcingulate cortex (aMCC). Subcortical activity was observed in the right thalamus and the right caudate nucleus (Fig. 1, Table S2).

3.2. Meta-analyses for the individual task types

Stroop task: Investigating consistent activation across the experiments using the Stroop task revealed significantly convergent activity in a bilateral network consisting of aI extending into IFG (pars orbitalis/triangularis), the intersection between posterior IFG and the precentral gyrus, i.e., the inferior frontal junction (IFJ), as well as the intraparietal sulcus, with a more wide-spread activity in the left hemisphere that extended into the SPL and IPC. Moreover, significant convergence was found in the preSMA extending into aMCC (Fig. 2A, Table S3). Furthermore, we ran a supplementary meta-analysis that only included those 47 experiments

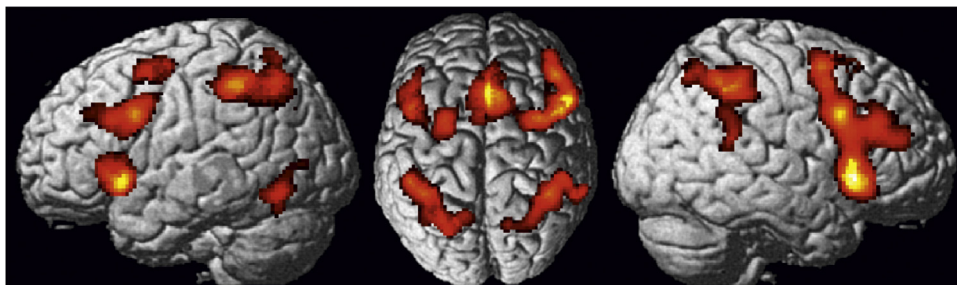


Fig. 1. Foci of brain activity showing significant convergence of activity across all experiments included (cluster-level $p < 0.05$, family-wise error-corrected for multiple comparisons, cluster forming threshold $p < 0.001$ at voxel level).

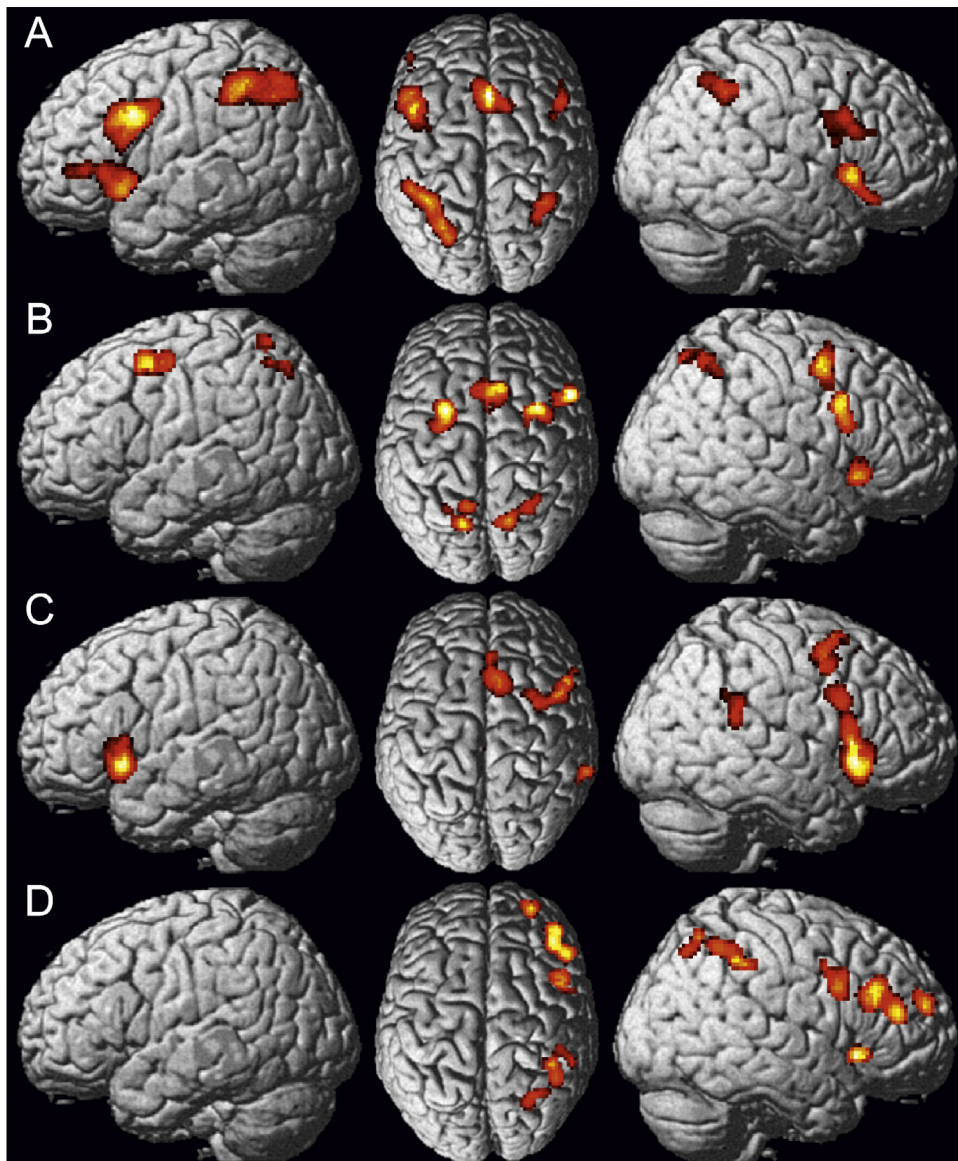


Fig. 2. Foci of brain activity showing significant convergence of activity for the four paradigm classes separately, the (A) Stroop, (B) spatial interference, (C) stop-signal and the (D) go/no-go task, (cluster-level $p < 0.05$, family-wise error-corrected for multiple comparisons, cluster forming threshold $p < 0.001$ at voxel level).

investigating the verbal version, i.e. the colour-word Stroop task. Even though this supplementary meta-analysis revealed slightly smaller clusters of convergence, this additional analysis did not change the overall results, but moreover showed significant convergence in the left inferior occipital gyrus (MNI coordinates: $-48/-59/-18$) (Fig. S1).

Spatial interference task: Investigating consistent activation across the experiments using spatial interference tasks revealed significant convergence of activity in a bilateral dorsal frontoparietal network consisting of dPMC and the superior parietal cortices. Moreover, significant convergence of activity was found in the right IFJ and adjacent IFG (pars opercularis), right aI and the aMCC extending into preSMA (Fig. 2B, Table S4).

Stop-Signal task: Performing a meta-analysis across experiments contrasting stop vs go trials in the stop-signal tasks revealed consistent activation in bilateral aI extending into IFG (pars opercularis), the aMCC, the preSMA and the posterior cingulate cortex (PCC). Moreover, right-lateralized activity was found in the IFJ, dPMC and TPJ. Subcortical activity was found in bilateral thalamus (Fig. 2C, Table S5).

Go/no-go task: Performing a meta-analysis across experiments contrasting no-go vs go responses in the go/no-go task showed consistent activity in a right-lateralized frontal network consisting of the DLPFC, the IFJ as well as the aI extending into the pars orbitalis of IFG. Moreover, parietal activity was found in the IPS extending into adjacent IPC as well as the SPL (Fig. 2D, Table S6).

3.3. Conjunction analyses

To isolate brain activity specifically related to supervisory attentional control, independent of task specifics, we performed a minimum conjunction analysis across the thresholded ALE maps of all four paradigm classes (cf. above). This analysis revealed significant convergence in two clusters: the right aI and right inferior frontal junction (Fig. 3, Table S7).

Subsequently, conjunction analyses were performed across the thresholded maps for all combinations of three paradigm classes: (i) Stroop AND stop-signal AND spatial interference tasks, (ii) Stroop AND go/no-go AND spatial interference tasks, (iii) go/no-go AND stop-signal AND spatial interference tasks, and (iv) Stroop AND

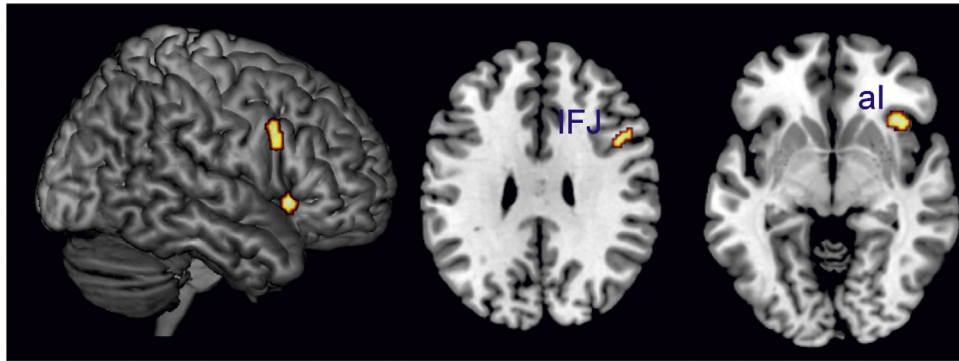


Fig. 3. Performing a minimum conjunction analysis across the four paradigm classes (Stroop, spatial interference, stop-signal and go/no-go task) revealed the right anterior insula and the right inferior frontal junction to be the only two regions showing conjoint convergence of activity across all four task types.

go/no-go AND stop-signal tasks. Thereby it was found that right al, right IFJ as well as the anterior mid-cingulate cortex and the preSMA were consistently involved in the Stroop, spatial interference and stop signal tasks (Fig. 4, Table S7). All other conjunction analyses did not reveal significant convergence of activity in any other region than the right al and right IFJ, i.e., the full conjunction reported above (Table S7).

Differences between the four task types were computed as well and are shown in the Supplementary Material (Fig. S2) as the focus of the present meta-analyses was to delineate the core regions consistently recruited across facets of cognitive action control.

4. Discussion

We used coordinate-based ALE meta-analyses to analyze the neural correlates of cognitive action control in different paradigms that all require the suppression of an inappropriate action and the concurrent initiation and execution of the context-appropriate alternative. In total, 173 experiments investigating go/no-go, stop-signal, Stroop and spatial interference paradigms were included. While the main effect across all experiments, independent of task type, revealed a broad bilateral frontoparietal network, the right al and the right IFJ were the only two regions that showed consistent involvement in all individual paradigm classes, as revealed by a minimum conjunction. Moreover, the aMCC and the preSMA were conjointly recruited by all but the go/no-go task. We hence suggest that the al and IFJ in the right hemisphere and the aMCC/preSMA play a pivotal role for the regulatory processes mediated by the SAS, while other frontal and parietal regions are associated more specifically with sub-components of cognitive action control that are differentially engaged in the respective paradigms.

4.1. Main effect of all included experiments

Performing a meta-analysis of all included experiments related to cognitive action control revealed consistent activity in a bilateral frontoparietal network consisting of the al and adjacent IFG, the DLPFC, dPMC and the IPS extending into the SPL. Moreover, convergent activity was found in the right TPJ and in the left inferior occipital gyrus as well as the aMCC extending into (pre)SMA. Of note, the aMCC has often been labelled “dorsal anterior cingulate cortex” in previous studies according to Brodmann’s well-known nomenclature. However, as there is convincing evidence of a structurally and functionally distinct middle cingulate cortex (cf. Palomero-Gallagher et al., 2009; Vogt et al., 2004; Vogt, 2005), we will here use the more precise term “aMCC” instead of the rather widely used but overly broad term “(dorsal) anterior cingulate cortex.” With the exception of the right temporoparietal junction, the present network closely resembles a network that has been found as the main effect of working memory in a recently published meta-analysis study (Rottschy et al., 2012). Another meta-analysis investigating sustained attention (Langner and Eickhoff, 2013) also found consistent involvement in a very similar network, which however showed less extended activity in the dPMC and IPS and was more lateralized to the right hemisphere. As inhibition, working memory as well as sustained and selective attention are regarded as core component factors underlying executive functions (Alvarez and Emory, 2006), this network most likely represents a set of cortical regions that interact with each other during executive control processes across a wide variety of tasks (cf. Müller et al., in press). Along the same lines, a very similar set of regions has been shown to be engaged across a diversity of cognitively demanding tasks and hypothesized to respond in a

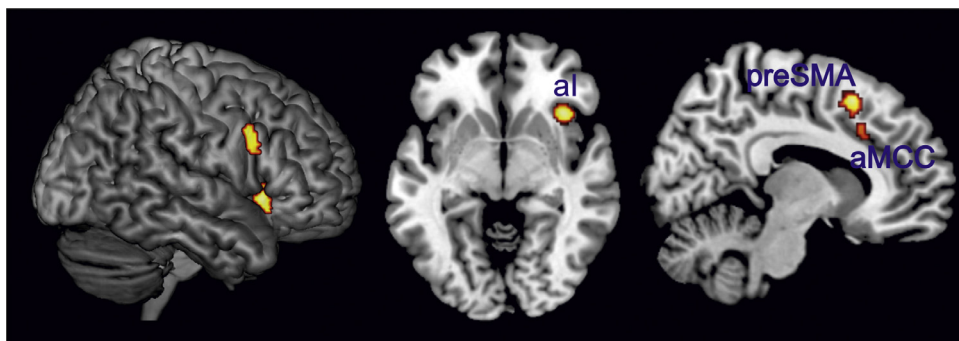


Fig. 4. Right al, right IFJ as well as anterior mid-cingulate cortex and preSMA were conjointly involved in the Stroop, spatial interference and stop-signal tasks as revealed by conjunction analysis.

domain- and process-general manner (Cole and Schneider, 2007; Duncan, 2010; Duncan and Owen, 2000; Fedorenko et al., 2013).

4.2. Conjunction analyses

Conjunction analyses were performed to isolate those brain regions that are consistently associated with the regulatory processes proposed to be mediated by the supervisory attentional system (Norman and Shallice, 1986; Stuss et al., 1995). All four paradigm classes required the implementation of a non-dominant, context-dependent behaviour against a competing behavioural alternative. Accurate performance in these tasks therefore requires performance monitoring as well as energization of the relevant, nondominant task schema. These processes have been proposed to be mediated by the SAS (Norman and Shallice, 1986; Stuss et al., 1995), but to date its underlying neural correlates have mainly been investigated using lesion studies. These studies revealed a crucial role of the right lateral prefrontal cortex for monitoring of ongoing performance, with exact location of lesion sites varying from the right lateral to the inferior PFC. In contrast, energization has been strongly associated with the posterior dorsomedial frontal cortex around Brodmann area 24, 9 and 6 (Stuss, 2006, 2011). However, lesion studies have a drawback: the mapping of functions to circumscribed anatomical regions is rather vague. Our conjunction analysis now specifically revealed the right IFJ and the right al to be the only two regions showing consistent activity across all four paradigm classes investigated. Moreover, all but the go/no-go task revealed consistent involvement of the aMCC and preSMA. Thus, the present results indicate that the al and IFJ in the right hemisphere as well as the aMCC/preSMA play a central role in supervisory attentional control.

The insula is a functionally heterogeneous region, hypothesized to exert an integrative role between the homeostatic, affective and cognitive systems of the human brain (cf. Craig, 2010; Kurth et al., 2010; Medford and Critchley, 2010; Menon and Uddin, 2010). With respect to its cognitive functions, Dosenbach and colleagues (Dosenbach et al., 2006, 2007) proposed that the al together with the aMCC/preSMA forms a core network for the implementation and stable maintenance of task sets. This view was based on their finding that this network showed reliable start-cue and sustained activation across a diversity of tasks. Recent studies using different methods support the assumption that especially the right al plays a critical monitoring role. For example, Sridharan et al. (2008) found that the right al plays a causal role in activating task-relevant regions while concurrently deactivating other regions, such as the default mode network, that are extraneous to the current task. It has hence been assumed that the right al acts as an “outflow hub” controlling 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). In line with that, functional imaging studies revealed evidence for a specific relation between al activity and task performance. In particular, an fMRI study of Wager et al. (2005) found a positive correlation of activity in the right al with task performance across three different tasks that were also investigated within the present meta-analyses (i.e., flanker, SRC, and go/no-go tasks). Bunge et al. (2002) also showed a positive correlation of right al activity with better task performance (i.e., less interference-related slowing of RTs) in a spatial flanker task. Summarizing, the al may thus monitor the activation of the relevant task set and, if necessary, sent a control signal to other task-relevant regions, such as medial prefrontal cortex as well as the parietal cortex to enable correct task performance in a moment-to-moment manner (cf. Dosenbach et al., 2008; Holmes et al., 1998; Langner and Eickhoff, 2013; Power and Petersen, 2013).

The right IFJ was the second region showing significant convergence of activity across all four paradigm classes. This region is

located at the junction of the inferior frontal sulcus and the inferior precentral sulcus (cf. Derrfuss et al., 2005) and has been implicated in task switching and set shifting paradigms but also in the Stroop or n-back task (Derrfuss et al., 2004, 2005). It has hence been discussed to mediate processes concerning the updating of task representations and specification of general task goals (e.g. Brass et al., 2005a, 2005b; Derrfuss et al., 2004, 2005; Kim et al., 2011). While these studies have consistently shown involvement of particularly the left IFJ, the present meta-analysis revealed consistent involvement of the right IFJ across task types. A recent study by Zheng et al. (2008) found a region located very close to our right IFJ cluster whose activity showed a significant positive correlation with participants' performance in two different tasks: it showed a positive correlation with the stop-signal reaction time in a stop-signal task and a negative correlation with the false alarm rate, which described the proportion of no-go trials on which participants failed to withhold their response in a go/no-go task.

Even though several other studies have shown activity within the right IFJ during the go/no-go, stop-signal or antisaccade tasks (Aron, 2011; Chikazoe et al., 2009) as well, the right IFJ has mainly been associated with the detection of changes in stimulus features as well as the detection of infrequent but action-related events (Chikazoe et al., 2009; Verbruggen et al., 2010). Although the probabilities of inhibition and go stimuli are often unequal in stop-signal and go/no-go tasks (i.e. inhibition trials are usually rarer), this does not necessarily hold for the interference paradigms. Hence, we argue that the right IFJ may not be selectively involved in the detection of infrequent events per se (see also Levy and Wagner, 2011). As the right IFJ was conjointly recruited across all tasks investigated, and participants were always required to integrate a bottom-up stimulus with a non-dominant motor response, we would rather suggest that the function of the right IFJ may go beyond simple detection. Interestingly, a recent meta-analysis investigating vigilant attention (Langner and Eickhoff, 2013) also found consistently stronger involvement in tasks with longer vigilant attention maintenance in the IFJ. Hence, it seems that the IFJ, especially in the right hemisphere, is associated with the continuous reactivating of the non-dominant but relevant S-R mapping against the automatic but inadequate action that has to be inhibited, such as responding to the word meaning in the Stroop task or responding to a left-sided stimulus with the left hand in SRC or Simon tasks (cf. Brass et al., 2005a; Derrfuss et al., 2005). We, therefore, propose that while the al is associated with the monitoring and general implementation of the relevant task set, the right IFJ is more specifically associated with the continuous reactivation of the relevant task rule that links relevant stimulus features and non-dominant responses in a task-specific manner.

Beside the IFJ and al, two other regions were rather consistently associated with inhibiting the predominant motor response and activating the context-dependent alternative: aMCC and preSMA were conjointly involved in all but the go/no-go task. Both of these regions have been found jointly involved in many tasks, which make a clear functional dissociation rather difficult. The aMCC has been proposed to mediate the interaction between motor intentions and motivational state (Paus, 2001). In line with this, a recent fMRI study revealed the aMCC to be the key region for volitional action control as this region showed increased activity for internal movement selection compared to reactive movements, with even higher activity when participants could not only choose which hand to use but could also choose the timing, i.e., when to perform the movement (Hoffstaedter et al., 2013). Moreover, the aMCC has been related to performance monitoring by detecting conflicts in information processing and – through interaction with other task-relevant regions – focusing attentional resources on task-relevant information and adapting behavioural plans according to task demands (for a review see Botvinick et al., 2004). The

adjacent preSMA has been more strongly associated with executive control of motor output, in particular response inhibition as well as selecting the appropriate response between different response alternatives (cf. Barber et al., 2013; Mostofsky and Simmonds, 2008; Nachev et al., 2008). Electrophysiological recordings in non-human primates also demonstrated a specific involvement of the preSMA in switching from an automatic to a controlled response (Isoda and Hikosaka, 2007). Moreover, tracing studies revealed strong anatomical connectivity with anterior premotor areas, area 24c in the cingulum, and the prefrontal cortex (Luppino et al., 1993) supporting the hypothesis that the preSMA is involved in higher cognitive control of motor behaviour. We therefore propose that differences between the aMCC and preSMA are most likely related to the conceptual level of cognitive control: while the aMCC is related to the detection of conflicting response plans on a higher cognitive level such as discerning competing response plans, the preSMA is more strongly associated with monitoring actual motor output by selecting the appropriate motor output (Nachev et al., 2008). The role of the aMCC/preSMA would then correspond to what Stuss and colleagues conceptualized as energization of the appropriate task schema (Stuss et al., 1995). That is, whenever stimuli or the motivational conditions are not optimal for responding, energization of lower-level systems by the posterior dorsomedial frontal cortex is needed (cf. Shallice et al., 2008a, 2008b). This process would come into play whenever the non-dominant task schema, such as responding incongruently in the Stroop task or initiating the stopping of an already started motor response in the stop signal task, needs to be “energized”.

Importantly, we did not find the left lateral PFC to be consistently involved across all four task types despite strong evidence from lesion studies that this region also plays a crucial role for supervisory attentional control, in particular for the sub-process of task-setting (e.g. Shallice et al., 2008a, 2008b; Stuss and Alexander, 2007). More specifically, it has been shown that patients suffering from left lateral PFC lesions show increased error rates particularly in the initial stages of learning a task (i.e., when new schemata need to be acquired), while performance becomes normal in later trials (Shallice et al., 2008a, 2008b). In line with that, an fMRI study by Hartstra et al. (2011) found the left lateral PFC including the IFJ to be specifically activated for the implementation of new compared to multiple applied task instructions. Similarly, Ruge and Wolfensteller (2010) found a practice-related activation decrease in the IFJ, with increased BOLD activity present in the first trials of newly instructed S-R mappings and a BOLD signal decrease to above baseline with increasing practice. These findings have been interpreted as showing a specific role of the left lateral PFC in task-setting, that is, setting the specific stimulus–response contingencies that will automatically control behaviour when the task becomes routine. In line with this notion, activity within the left lateral PFC, particularly the left IFJ, has also consistently been shown during various forms of task switching where participants have to constantly update and switch the actual relevant task set (Brass and von Cramon, 2004; Derrfuss et al., 2005; Kim et al., 2012). As the neuroimaging studies included in our meta-analyses did not examine differences in BOLD fluctuations between the beginning of a block (i.e. the learning phase) and the phase when participants perform the task in a more automated fashion, this might have driven our finding of no consistent involvement of left lateral PFC across all task types investigated. Interestingly, the Stroop task was the only task that revealed consistent involvement of left lateral PFC including IFJ in the single-task analysis. This is in line with a previous meta-analysis that found consistent involvement of left IFJ in the Stroop task (Derrfuss et al., 2005). A possible reason for this bilateral finding for the Stroop task might be the verbal character of the task, which may lead to stronger recruitment of left-sided prefrontal regions. Another explanation comes from behavioural and

neuroimaging studies showing that in the Stroop task two types of conflict play a role: (i) informational (or response) conflict between the contradictory information that arises from the word meaning and the information that arises from the word colour, and (ii) task conflict, i.e. a conflict between the relevant identification of the colour naming task and the irrelevant but automatic reading task (Goldfarb and Henik, 2007; Kalanthroff et al., 2013). As such, the Stroop task requires some form of task-setting or, more particularly, switching between two task sets throughout the task, leading to consistent recruitment of left lateral PFC in this task type.

In summary, we showed that the right aI, IFJ and aMCC/preSMA are consistently found in tasks requiring cognitive control over a predominant response tendency. While previous studies have commonly proposed the PFC to exert specific inhibitory control over other brain regions, we argue that these core regions implement inhibitory control rather indirectly by monitoring the relevant task set and enhancing goal-relevant processing whenever the predominant task schema does not agree with the superordinate behavioural goal (see also Munakata et al., 2011). This interpretation also has implications for patients with frontal lobe lesions or psychiatric disorders such as schizophrenia or attention deficit hyperactivity disorder, where abnormal task performance has commonly been interpreted as a deficit in inhibitory action control (Aron et al., 2003a,b; Broerse et al., 2001; Depue et al., 2010; Rubia et al., 2010). However, it seems that rather than being caused by a failure of directed global inhibition, response errors in these patients may be more strongly related to a failure to monitor and implement the relevant task set (see also Everling and Johnston, 2013; Langner et al., 2014; Munakata et al., 2011).

4.3. Individual task analyses

In addition to the consistently recruited regions discussed above (i.e., right aI, right IFJ, and aMCC/preSMA), several other regions were selectively recruited by distinct paradigm classes. These paradigm-specific foci will be discussed in the following.

4.3.1. Stroop task

For the Stroop task, significant convergence of activity was found bilaterally in aI/IFG, dorsal-posterior IFG, parietal cortex as well as the aMCC/preSMA (Fig. 2A).

Interestingly, a strongly bilateral network was found for the Stroop task, despite the task's verbal character. It has to be noted that in the present meta-analysis we not only included colour-word Stroop experiments but also slightly different versions such as the numerical Stroop, which may have driven the more bilateral activity. We therefore ran a supplementary meta-analysis across Stroop tasks only including those 47 experiments investigating the classic colour-word version. As can be seen in Fig. S1, even though activations were less extended, this analysis did not change the overall results. That is, even when the analysis was restricted to colour-word Stroop tasks, we found a largely symmetric bilateral network. We therefore suggest that performance in the Stroop task relies on a bilateral network, in particular within the prefrontal and parietal cortices.

While most studies have emphasized the role of the frontal cortex and aMCC in the Stroop task as substrates of conflict processing and cognitive control during incongruent responding (cf. Derrfuss et al., 2005; Laird et al., 2005), we also found consistent involvement of parietal regions. Moreover, when only including the colour-word version of the Stroop task, additional convergence of activity was found in the left inferior occipital gyrus. In particular, convergence of activity in the left inferior occipital cortex was located very closely to the visual word form area (McCandliss et al., 2003) that has consistently been related to the perceptual processing of visual letter stimuli (James et al., 2005; Vinckier et al., 2007).

We therefore propose that the left inferior occipital cortex is most likely related to a (top-down modulated) increase in the sensory analysis of the stimulus when word meaning and word colour are incongruent.

Parietal foci were located in bilateral medial IPS, in particular area HIP3 (Scheperjans et al., 2008a, 2008b). The medial part of the IPS has been discussed to play a critical role in the selection between competing stimuli as well as different stimulus features (Gillebert et al., 2013a, 2013b; Molenberghs et al., 2007; Vandenberghe et al., 2005). In the Stroop task, the automatic tendency to read the word interferes with the task instruction to name the colour of the word. Convergence of activity for the Stroop task in bilateral IPS would thus most likely be related to the selection of the relevant stimulus features when participants are required to focus their attention on the colour of the word while inhibiting the automatic reading. In turn, the IPS may then represent the source of top-down (attentional) signals modulating the processing in earlier visual cortices, i.e., the aforementioned occipital effect.

4.3.2. Spatial interference tasks

In the spatial interference tasks, convergence of activity was found in a bilateral frontoparietal network consisting of the dPMC and SPL as well as the right IFJ and adjacent IFG, right aI, and aMCC/preSMA.

The parietal lobe (around the IPS and SPL) and the dorsal frontal cortex along the precentral sulcus have been proposed to form a dorsal attention network (Corbetta et al., 2008; Corbetta and Shulman, 2002). Increased activity in this network has been shown during spatially incompatible responding (Cieslik et al., 2010; Schumacher et al., 2003) and in relation to attentional reorienting and increased demands of S-R mapping and redirecting of response intentions (e.g. Mars et al., 2007; Rushworth et al., 2003; Sylvester et al., 2003). All paradigms subsumed under the label “spatial interference tasks” in the present study require resolution of spatial conflicts for successful responding. In all these paradigms, an automatic reorientation of attention and response preparation in the direction of the spatial stimulus dimension is induced. Participants then need to reorient their focus of attention to perform adequately and initiate a response to a non-dominant spatial location. Consistent involvement of the dorsal attention network across these tasks should thus reflect an increased need for controlled spatial processing when participants intentionally reorient attention as well as response intentions to adequately respond in a spatially incongruent manner.

Interestingly, the present meta-analysis revealed consistent involvement of area 7A (Scheperjans et al., 2008a, 2008b) in the SPL. This in line with previous fMRI studies that revealed a crucial role for the SPL in shifting the locus of spatial attention (Capotosto et al., 2013; Vandenberghe and Gillebert, 2013; Vandenberghe et al., 2001) but less involvement of the SPL when stimulus features change without spatial shift (Molenberghs et al., 2007). The present study moreover showed a differential involvement of posterior parietal cortex in the Stroop and spatial interference tasks (Fig. S2C). In particular, the medial IPS showed stronger convergence for the Stroop task, while the SPL (area 7A) showed stronger convergence for spatial interference tasks. This finding may well be related to functional imaging studies showing a differentiation within the parietal cortex for attentional shifts. Thereafter, the middle IPS has been associated with the selection between competing stimuli (Gillebert et al., 2013a, 2013b; Vandenberghe et al., 2005), and feature attention shifts (Molenberghs et al., 2007). In contrast, the SPL is specifically activated during spatial shifts of attention such as when a spatial displacement occurs in the location of the target or the focus of attention (Capotosto et al., 2013; Molenberghs et al., 2007; Vandenberghe et al., 2001) but less strongly so when stimulus features change without spatial shifts (Molenberghs et al.,

2007). Hence, differential parietal involvement when comparing the Stroop and spatial interference tasks in the present meta-analysis might reflect differences in attentional shifting demands, with spatial attention shifts required in spatial interference tasks and feature attention shifts required in the Stroop task.

4.3.3. Stop-signal task

In the stop signal task convergent increased activity for motor response inhibition versus responding was found in the bilateral aI extending into posterior IFG on the right side as well as the right IFJ, dPMC and TPJ. Moreover, the aMCC, preSMA/SMA, posterior cingulate cortex, as well as bilateral thalamus showed significant convergence of activity (Fig. 2C). Interestingly, the right TPJ, posterior cingulate cortex and thalamus were only found for the stop signal tasks but were not consistently associated with any other task type. Conceptually, stop signal tasks differ from the other task types in that they require inhibiting or, rather, cancelling an already initiated motor response, while the go/no-go, Stroop and spatial interference tasks require suppression of a dominant but not yet initiated action. Successful inhibitory control in stop signal tasks requires attentional capture and evaluation of the relevant stop cue and inhibition of the (already initiated) motor response (Logan et al., 1997). The right TPJ – together with the right frontal cortex – has been suggested to form a ventral attention network that is associated with the (re)direction of attention to behaviorally relevant stimuli outside the current focus of attention (Corbetta et al., 2008; Corbetta and Shulman, 2002; Fox et al., 2006). A recent review, however, proposed a more global role of the right TPJ based on evidence that this area is related to the integration of stimulus information with internal models of task performance and expectations, thereby playing a pivotal role in contextual updating (Geng and Vossel, 2013). In line with this view, the right TPJ has been associated with predictive motor coding, including the updating of action expectations and the comparison of pre-prepared programs with current task requirements (cf. Eickhoff et al., 2011; Jakobs et al., 2009) as well as updating of temporal predictions of the onset of the next stimulus and its associated response (Langner et al., 2012). With respect to the stop signal task, consistent involvement of the right TPJ would thus most likely be associated with the updating of the context and its associated response when the stop signal is “captured” in the attentional focus, indicating the need to inhibit the already initiated motor response.

In addition, the two other regions that were consistently recruited only by the stop signal tasks, the dorsal PCC and thalamus, have recently been shown to be part of a network specifically associated with the cancellation of already initiated actions (Dambacher et al., 2014). Even though a recent meta-analysis (Swick et al., 2011) also showed consistent involvement of the PCC in the stop signal task, and other authors found stronger involvement of this region in successful compared to failed inhibition (Li et al., 2006), the functional role of this region in the context of response inhibition has rarely been discussed. Rather, the PCC is best known for its central role within the default mode network, a set of brain regions showing strongly correlated activity during the resting state and consistent deactivation during divergent cognitive control tasks (Buckner et al., 2008; Buckner and Carroll, 2007; Raichle et al., 2001; Schilbach et al., 2012). Anatomical evidence and network analyses, however, support the assumption that the PCC is not a homogenous region but can be divided into a dorsal and ventral subregion that differ in their cytoarchitectonic organization as well as their functional properties and network dynamics (Leech et al., 2011; Leech and Sharp, 2014; Vogt et al., 2006). While both subregions show resting state functional connectivity (RS-FC) with the default mode network, the dorsal PCC moreover reveals RS-FC with regions strongly related to cognitive control (Leech et al., 2011). Furthermore, the dorsal PCC has been proposed to play a

key role in maintaining a broad attentional focus thereby being able to alter behaviour in response to unexpected changes in the environment that are not part of the current cognitive set (cf. Leech and Sharp, 2014; Pearson et al., 2011). With regard to the present results, this interpretation would be in agreement with dorsal PCC involvement for successful inhibition in the stop signal task when a delayed stimulus in the environment has to be detected. Here it would mediate between internal and external attentional focus to successfully integrate the delayed stop stimulus with the current attentional focus and task set (Leech et al., 2011).

Additionally, the finding of consistent involvement of the thalamus in the stop signal task relates well to other studies showing that the thalamus increases activity during response inhibition (Aron and Poldrack, 2006; Aron et al., 2003a,b; Bellgrove et al., 2004) and suggesting that it plays a key role for successful versus failed inhibition (Li et al., 2006). Moreover, the thalamus seems to be specifically involved in active action cancellation as a recent fMRI study found the thalamus to be more activated when cancelling actions in the stop signal task versus restraining of actions in the go/no-go task (Dambacher et al., 2014). In the present study, consistent activity was specifically found in that part of the thalamus which is anatomically connected with the prefrontal cortex as shown by diffusion data (Behrens et al., 2003), suggesting that this part of the thalamus together with the prefrontal cortex might form a cortical circuit related to the control of response inhibition and specifically comes into play when already initiated motor plans have to be cancelled (see also Aron, 2011; Dambacher et al., 2014).

4.3.4. Go/No-Go task

The go/no-go task was associated with consistent activity in a right-lateralized frontal network consisting of anterior and posterior DLPFC, IFJ, as well as al extending into the IFG. Moreover, consistent parietal activity was found in the IPS extending into adjacent IPC and SPL (Fig. 2D).

Interestingly, the regions consistently involved in the go/no-go task differed to some extent from the results of the stop signal task even though these two tasks have been discussed very similarly in the literature (cf. Verbruggen and Logan, 2008). The present study, however, provides evidence for differential networks involved in withholding versus cancelling responses (Fig. S2D). In particular, action withholding is consistently linked to activity in the right anterior and posterior DLPFC as well as extended activity in right parietal cortex (covering IPS, SPL and IPC) (Fig. 2D). To further characterize lateral prefrontal foci in the go/no-go task, anterior and posterior DLPFC cluster were compared with sub-regions in the dorsolateral frontal cortex recently identified using tractography-based parcellation by Sallet et al. (2013). While our posterior DLPFC cluster is located in *cluster 6/Area9/46v* as defined by Sallet et al., our anterior cluster was localized in their *cluster 7/Area 46*.

The (right) DLPFC has been associated with choosing responses based on rules (cf. Ridderinkhof et al., 2004) and the selection of items from working memory (Rowe and Passingham, 2001; Rowe et al., 2000). The DLPFC shows strong anatomical connections with the parietal lobes as well as motor system structures (Bates and Goldman-Rakic, 1993; Cavada and Goldman-Rakic, 1989; Lu et al., 1994; Petrides and Pandya, 1984, 1999; Schmahmann and Pandya, 1997), thereby lying in a perfect position to monitor behaviour by mediating which S-R association has to be implemented in a given context (Miller and Cohen, 2001). The present study reveals that two different parts of the DLPFC – an anterior part and a posterior one – show consistently stronger involvement in no-go compared to go conditions (Fig. 2D). Hierarchical models propose an anterior–posterior gradient in the PFC for executive control processes (Badre and D'Esposito, 2009; Koehlin and Summerfield, 2007), with more anterior parts of lateral PFC involved in the

representation of more abstract schemata such as context and future tasks, while more posterior parts of lateral PFC are associated with the implementation of instructions and rules into actual motor output (for a review see Courtney, 2004). In line with that, we propose that the more anterior foci in the present study may be related to the representation of contextual information such as task instructions, while the more posterior foci may implement which S-R (or stimulus–stop) association needs to be assessed in the respective condition (cf. Simmonds et al., 2008). This would then be performed conjointly with the parietal cortex, which is assumed to integrate 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 go/no-go tasks in the present meta-analysis as well as in previous ones (Simmonds et al., 2008; Swick et al., 2011).

Interestingly, the go/no-go task was the only task that did not reveal a consistent involvement of the aMCC and preSMA in cognitive action control. In contrast, two previous meta-analyses did find consistent recruitment of the preSMA for the go/no-go task (Simmonds et al., 2008; Swick et al., 2011). This discrepancy might be driven by different factors. For example, the two other meta-analyses included a smaller number of studies (11 and 21 experiments respectively) and used less conservative thresholds. More importantly, however, selection criteria differed between those studies and our study: as both previous meta-analyses also included experiments using “no-go vs. baseline” or “no-go vs. fixation” contrasts, respectively, while in the present meta-analysis only “no-go vs. go” contrasts were included. Hence, given that “go”-conditions also recruit the aMCC/preSMA, the probability to find consistent activity in aMCC/preSMA was much higher in the two previous studies. Our results reveal that the aMCC and preSMA are not consistently more strongly involved in no-go versus go responses. This might be explained by the fact that in the no-go condition participants have to withhold a motor response without initiating an alternative action. Integrating our results with those from the two previous meta-analyses (Simmonds et al., 2008; Swick et al., 2011) we suggest that response withholding indeed does consistently recruit the aMCC/preSMA, but not to a stronger degree than does the initiation of a go-response.

5. Conclusion

In this study, we investigated the neural substrates of cognitive action control via coordinate-based ALE meta-analyses of brain activity reported for Stroop, spatial interference, stop-signal, and go/no-go tasks. Our study provides evidence for a pivotal role of the right al and right IFJ in supervisory attentional control, because these were the only two regions consistently involved in all four paradigm classes, as revealed by a minimum conjunction analysis. Furthermore, aMCC and preSMA were commonly recruited by all but the go/no-go task. In contrast to previous studies that proposed the PFC to exert specific inhibitory control over other brain regions, we argue that these core regions implement inhibitory control rather indirectly by monitoring the relevant task set and exciting goal-relevant processing areas whenever the predominant task schema does not agree with the superordinate behavioural goal. Following the conceptual model of Stuss, Shallice and colleagues (Stuss, 2011; Stuss et al., 1995), we would argue that the al and IFJ in the right hemisphere support schema activation monitoring processes, with the al playing a crucial role in monitoring and general implementation of the relevant task set, while the right IFJ is more specifically associated with the continuous reactivation of the relevant S-R rule. The aMCC/preSMA, on the other hand, is thought to mediate energization of the adequate (general) task schema.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.neubiorev.2014.11.003>.

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