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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 subprocesses 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