Localizing performance of go/no-go tasks to prefrontal cortical subregions

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Purpose of review

Response inhibition is an essential executive function implemented by the prefrontal cortex. Performance of go/no-go tasks, which are frequently used to investigate response inhibition, recruits a variety of cognitive components besides response inhibition. This article reviews recent findings on the functional localization associated with go/no-go tasks.

Recent findings

Recent neuropsychological and neuroimaging studies have shown that the presupplementary motor area and ventrolateral prefrontal cortex are crucial for response inhibition and that various subregions of the prefrontal cortex make different contributions leading to successful response inhibition. In particular, functional dissociation has been identified in the right ventrolateral prefrontal cortex, which consists of at least three subregions: the posterior part of the inferior frontal gyrus, inferior frontal junction and inferior frontal gyrus/insula.

Summary

Neuropsychological studies provide strong evidence that separate subregions of the prefrontal cortex make critical contributions to specific cognitive components involved in response inhibition, whereas neuroimaging studies cannot provide direct evidence regarding the causality, but provide insights into functional localization with high spatial resolution. These methods contribute significantly to our understanding of how executive functions are implemented and should continue to do so into the future.

Keywords

attention, functional localization, hemispheric laterality, response inhibition

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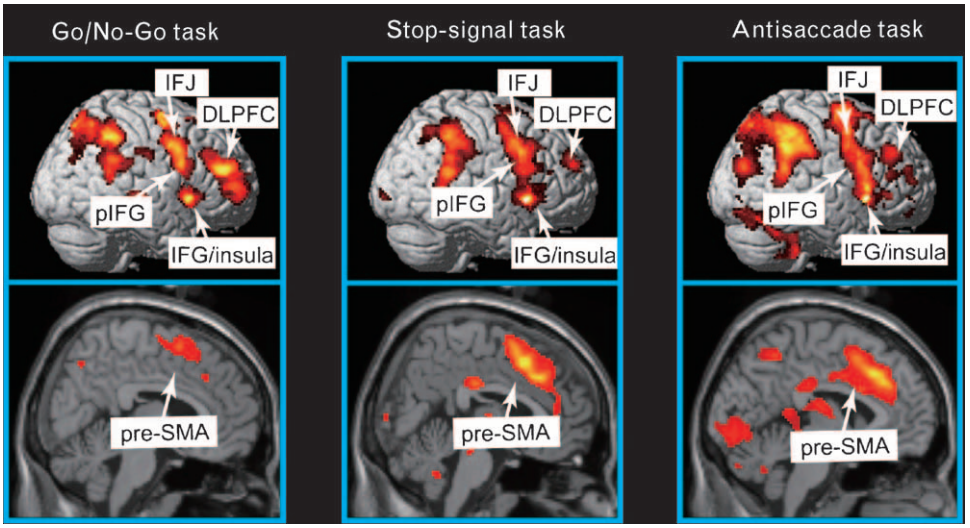
Introduction

Response inhibition is an essential executive function in humans and nonhuman primates. To investigate response inhibition, researchers commonly employ a go/no-go task, in which participants are required to respond to a go stimulus as quickly as possible, but are required to withhold their response to a no-go stimulus. Performance of a go/no-go task requires recruitment of a variety of cognitive components, including working memory, stimulus-driven attention (reorienting of attention), error monitoring, top-down control processes and response inhibition. Moreover, evidence from neuropsychological and neuroimaging studies has revealed the functional localization associated with these cognitive components. For example, recent neuropsychological [1] and transcranial magnetic stimulation (TMS) [2] studies provide strong evidence that the ventrolateral prefrontal cortex (VLPFC) plays a critical role in response inhibition, which is consistent with a broad range of neuroimaging studies that employed go/no-go tasks (for a meta-analysis, see [3]). Neuroimaging studies have also shown that, in addition to the VLPFC, performance of the go/no-go task recruits both the dorsolateral prefrontal cortex (DLPFC) and the presupplementary motor area (pre-SMA). Interestingly, recent studies employing stop-signal and antisaccade tasks, which are also commonly used to investigate response inhibition, have shown very similar activation patterns [4,5••,6] (Fig. 1), suggesting that these tasks inherently test the same cognitive processes (i.e. response inhibition). In this article, I will review the latest developments in functional localization within the prefrontal cortex associated with go/no-go tasks, paying particular attention to the functional organization of subregions within the VLPFC.

Ventrolateral prefrontal cortex plays a central role in response inhibition

The VLPFC appears to be essential for successful response inhibition (for recent reviews, see [7,8••]). One previous neuropsychological study found that response inhibition during performance of a stop-signal task is disrupted in patients by damage to the right

Figure 1 Similar activation patterns observed across three different paradigms



The go/no-go, stop-signal and antisaccade tasks consistently elicited activation of multiple brain regions, including the posterior part of the inferior frontal gyrus (pIFG), inferior frontal junction (IFJ), insula/inferior frontal gyrus (insula/IFG), dorsolateral prefrontal cortex (DLPFC) and presupplementary motor area (pre-SMA). Maps of the activation during performance of go/no-go, stop-signal and antisaccade tasks were revealed by contrasting no-go vs. frequent-go, stop vs. certain-go, and antisaccade vs. baseline-saccade trials, respectively. The reported activation cleared a significance threshold of *P* value less than 0.001. Activation maps were generated from data in [4,5••,6].

VLPFC and that the extent of the lesion correlated with the extent of the impairment of response inhibition [1]. It has also been shown that application of TMS to the right VLPFC disrupts response inhibition, but TMS application to several other brain regions, including the left inferior frontal gyrus (IFG), DLPFC, dorsal premotor cortex and right angular gyrus, does not, which suggests that the right VLPFC is specifically involved in response inhibition [2]. Consistent with that idea, information with higher spatial resolution obtained through neuroimaging has consistently shown the involvement of the VLPFC in response inhibition [9–13,14•–16•].

Although the VLPFC is a large region composed of several heterogeneous subregions (i.e. BA 6, 44, 45, 46 and 47), the functional organization within the VLPFC has rarely been investigated. That said, recent neuroimaging studies have shown that subregions within the VLPFC play different roles in mediating response inhibition [5••]. Below I will consider the specific functions of three of those subregions: the posterior part of the IFG (pIFG), inferior frontal junction (IFJ) and IFG/insula.

Posterior part of the inferior frontal gyrus is a potent candidate for the core region of response inhibition

Previous go/no-go studies have repeatedly shown activation within the VLPFC, particularly with the pIFG [3], which is reportedly associated with response inhibition. On the other hand, the IFJ, which is located at the border of the inferior frontal sulcus and precentral sulcus, is associated with the processing of infrequent stimuli [5••]. This suggests that the core region involved in response inhibition is likely the pIFG, not the IFJ. Although the IFJ and pIFG are situated close to one another and activation of these regions is often observed as a cluster, dissociation of the pIFG from the IFJ is supported by diffusion-weighted imaging studies of the connectivity between brain regions based on white matter trajectories [11,17]. Those studies show that the IFJ is connected to the SMA [17], whereas the pIFG is connected to the pre-SMA [11,17]. The pIFG also plays an important role as a part of an attention network. Based on the patterns of activation under different conditions, Corbetta and coworkers [18,19••] posited that a dorsal frontoparietal network, including the intraparietal sulcus (IPS) and the frontal eye field (FEF), embodies a top-down control mechanism, whereas a ventral frontoparietal network, including the pIFG, IFJ, IFG/insula and temporoparietal junction (TPJ), is associated with reorienting of attention. Moreover, although segregation of the dorsal attention network from the ventral one is nearly complete, spontaneous activity in the pIFG correlates with activity in both networks, suggesting that the pIFG may be a link between the two [20]. Adding to the results of the neuroimaging studies are electrocorticographic recordings made while a participant performed a stop-signal task, which confirmed the importance of the right pIFG during response inhibition [21••]. This study showed that the right pIFG response at the β-frequency (~16 Hz) was greater in successful stop trials than in

unsuccessful ones, which further confirms the contribution made by the pIFG to successful response inhibition. Taken together, the findings summarized in this section make the pIFG a good candidate for a core region mediating response inhibition.

Inferior frontal junction is associated with stimulus-driven attention

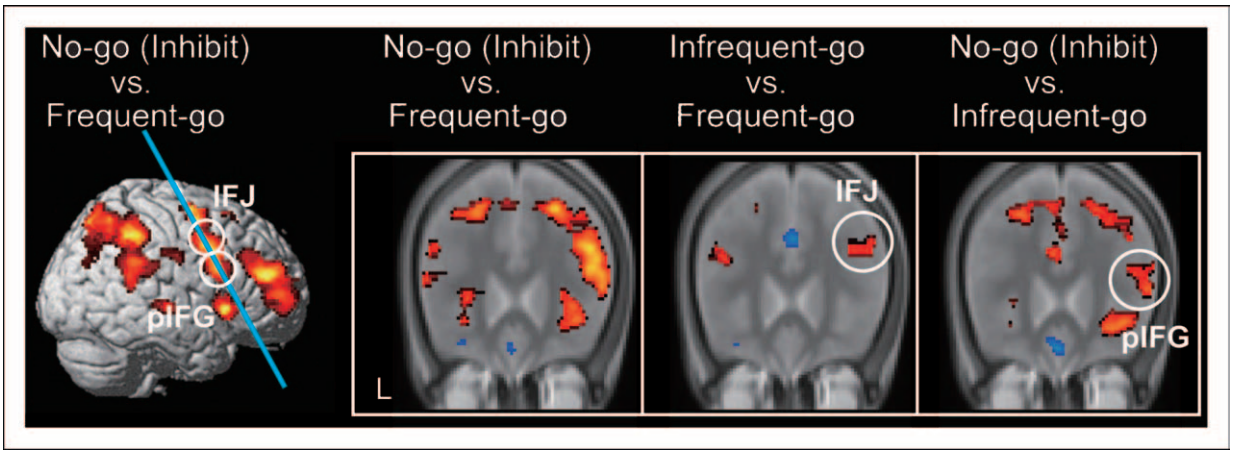
As mentioned, the IFJ is located at the junction of the inferior prefrontal sulcus and the inferior frontal sulcus. The involvement of the IFJ in stimulus-driven attention has been demonstrated in studies employing go/no-go, stop-signal and oddball tasks [14•,16•,22,23]. In the go/no-go paradigm, no-go trials are usually given infrequently relative to the go trials in order to enhance prepotent response tendencies; presenting the go and no-go trials in equal proportions would likely weaken the response inhibition in the no-go trials. Consequently, the cognitive components involved in the processing of infrequent stimuli, such as stimulus-driven attention, which should be separate from inhibitory processes, also come into play in the no-go trials. A recent study that employed both frequent and infrequent go trials was able to dissociate response inhibition (revealed by contrasting the no-go vs. infrequent-go trials) from the processing of infrequent stimuli (revealed by contrasting the infrequent-go vs. frequent-go trials) (Fig. 2) [5••]. The results revealed that, whereas the pIFG was associated with response inhibition, the IFJ was associated with processing of infrequent stimuli.

One important difference between cognitive components that activate the IFJ or pIFG might be task relevancy. Stimulus-driven attention is recruited in both the infrequent-go and no-go trials because both are given infrequently. In the infrequent-go trials, however, participants are not required to change behavior (i.e. participants respond as in the frequent-go trials), but they are required to change behavior in the no-go trials (i.e. participants must withhold a button press, which is performed in the frequent-go trials). Imaging results indicate that the pIFG is activated only in the no-go trials, not in the infrequent-go trials. By contrast, the IFJ is activated in both the infrequent-go and no-go trials. This suggests the IFJ is activated by reorienting of attention, irrespective of the behavioral change, whereas the pIFG is activated by reorienting of attention only when a behavioral change is required. Thus, the pIFG appears to play a specific role in response inhibition, whereas the IFJ plays a more general role associated with attentional control.

Inferior frontal gyrus/insula is associated with task invariant components

It has frequently been reported that response inhibition is associated with activation of the IFG/insula [3,4,5••,6,9,11–13,14•,16•], which is located at the border of BA 47 and the insular cortex. But because activation of this region often extends across both BA 47 and the insula, it is unclear whether activation of this region belongs to the IFG or the insular cortex [24]. Indeed, studies exploring common brain regions affected by various tasks often reported activation of the IFG/insula. For instance, Leung and Cai [25] found that the IFG/insula is involved in the performance of both ocular and manual stop-signal tasks. Activation of the IFG/insula is

Figure 2 Different activation patterns observed in the posterior part of the inferior frontal gyrus and inferior frontal junction in the inferior frontal cortex



Contrasting no-go vs. infrequent-go mainly activated the posterior part of the inferior frontal gyrus (pIFG), whereas contrasting infrequent-go vs. frequent-go mainly activated the inferior frontal junction (IFJ). The reported activation cleared a significance threshold of *P* value less than 0.001. Reprinted with permission from Oxford University Press Inc. [5••].

also reportedly involved in response inhibition elicited under different conditions [13,16•] and across different inhibition and working memory tasks. For instance, McNab *et al.* [24] showed that the IFG/insula is activated during two different working memory tasks (spatial and verbal), one cognitive inhibition task (flanker) and two response inhibition tasks (go/no-go and stop-signal). It is noteworthy that activation of this region is not specific to response inhibition. The IFG/insula is also associated with attention; cognitive choices and intentions; music; time perception; and awareness of sensations and movements, visual and auditory percepts, visual images of the self, and the trustworthiness of other individuals (for a thorough review, see [26•]). Based on evidence from a broad range of fields, Craig [26•] posited that the only feature common to all of these tasks is engagement of the individual's awareness. Another conjunction analysis across 10 different tasks revealed the sustained activation of the IFG/insula during the task period, suggesting that the IFG/insula forms a core task-set system [27]. Thus, though the IFG/insula may contribute to response inhibition, its function may not be specific for that purpose.

Presupplementary motor area is another critical region for response inhibition

The pre-SMA is thought to be another key locus of response inhibition. For example, one neuropsychological study employing a stop-signal task demonstrated that response inhibition is impaired following damage to the medial prefrontal cortex, including the right pre-SMA [28]. Another employing a go/no-go task demonstrated that patients with lesions to the pre-SMA had increased numbers of incorrect responses to no-go stimuli [29]. In addition, a recent TMS study confirmed that event-related TMS delivered over the pre-SMA disrupts response inhibition during performance of a stop-signal task [30••], whereas neuroimaging studies showed that there is robust activation of the pre-SMA during response inhibition, irrespective of whether the task structure is simple or complex [31], or whether the modality of the output is spoken or manual [13].

Although the pre-SMA undoubtedly plays a critical role in response inhibition, some researchers have pointed out the similarity between response inhibition and response selection. In a recent review, for example, it was suggested that, based on neuroimaging, TMS and lesion studies, it appears that response inhibition and response selection both emerge through a highly overlapping neural mechanism [32]. It was, therefore, suggested that pre-SMA circuits are critical for selection of appropriate behavior, including both selecting to engage appropriate motor responses and selecting to withhold inappropriate motor responses. That said, other TMS [2] and pharmacological [33] studies indicate that neural correlates of response selection and response inhibition do not totally overlap. Coxon *et al.* [34] reported that the pre-SMA participates in conflict resolution when movement is selectively prevented, which may indicate that the pre-SMA resolves preresponse conflict during selective movement prevention.

The medial prefrontal cortex is also known as a region associated with error processing [35]. However, error processing appears to be implemented by the anterior cingulate cortex (ACC), which is located ventral and anterior to the pre-SMA [36]. This view is supported by a previous go/no-go study showing that activation of the ACC was related to error processing, whereas activation of the pre-SMA was sensitive to the conflict manipulation [37]. Taken together, these findings support the notion that the pre-SMA makes a crucial contribution to response inhibition, acting in concert with the pIFG.

Dorsolateral prefrontal cortex may be related to top-down control processes

Activation of the DLPFC is consistently observed in individuals performing a go/no-go task [5••,14•,22]. This might be attributable to working memory demands, as significant DLPFC activation was observed during a counting go/no-go task, but not during a simple go/no-go task [38]. A recent conjunction analysis of a range of inhibition (i.e. go/no-go, stop-signal and flanker) and working memory (i.e. spatial and verbal working memory) tasks revealed that DLPFC activation is a common feature of these tasks, suggesting that common cognitive components function across response inhibition and working memory tasks [24]. On the other hand, studies have also shown that the DLPFC is associated with cognitive control [39] or top-down attentional control [22]. One recent study employing a modified go/no-go task revealed that high levels of top-down control, as indexed by DLPFC activation prior to the no-go trials, resulted in lower levels of activity in the pre-SMA on the no-go trials, which suggests that the lateral and medial prefrontal subregions work together to implement cognitive control [40•]. Although the specific role of the DLPFC has not yet been defined, it may be associated with top-down control processes during performance of a go/no-go task.

Hemispheric asymmetry

The available neuropsychological evidence suggests that the right VLPFC is critical for response inhibition [1]. Consistent with that idea, several neuroimaging studies have shown that response inhibition dominantly recruits frontoparietal networks in the right hemisphere, particularly in the pIFG [4,9,12]. This view is further supported

by attention research that suggests the importance of the right frontoparietal networks during attentional control [18,19••]. However, other neuropsychological studies found that the left VLPFC [41] or pre-SMA [29] is also critical for successful response inhibition. Notably in that regard, damage to one hemisphere can have an impact on brain activity in the intact contralateral hemisphere. For example, it was shown that spatial attention deficits after right frontal damage correlated with abnormal activation of structurally intact dorsal and ventral parietal regions mediating attentional operations in the normal brain [42]. This suggests that an interhemispheric functional imbalance may cause behavioral deficits, consistent with the hypothesis that the rightward bias in neglect is caused by a left hemisphere-orienting mechanism that is relatively hyperactive [43]. Functional connectivity across hemispheres is also disrupted following unilateral damage [44], and a significant correlation was observed between behavioral deficits and disruption of interhemispheric functional connectivity in the parietal cortex. It is, thus, plausible that damage to the left IFG or pre-SMA causes behavioral deficits via functional imbalance or disrupted functional connectivity across hemispheres.

Conclusion

Information gleaned from recent neuroimaging, neuropsychology and TMS studies extends our understanding of functional localization within the prefrontal cortex. As reviewed in this article, the VLPFC and pre-SMA are crucial for performance of a go/no-go task. In addition, neuroimaging techniques can now resolve functional organization on a subcentimeter scale, suggesting that future research may reveal prefrontal subregions on that scale [45••]. It may also be possible to shed new light on the heterogeneity of the VLPFC through application of TMS to the IFJ, pIFG and IFG/insula in individuals performing a go/no-go or stop-signal task. Understanding the inhibitory circuits at the network level is also important. An investigation of functional connectivity has demonstrated the distinct roles played by the pre-SMA and VLPFC during response inhibition [46•]. That study showed that signaling between the pre-SMA and primary motor cortex via basal ganglia circuitry is involved in mediating response inhibition, and stop success trials evoked greater effective connectivity between the pre-SMA and VLPFC than stop error trials. Further analysis of functional localization and the connectivity between prefrontal subregions should make important contributions to our understanding of the neural mechanisms underlying response inhibition.

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