

Attentional orienting and response inhibition: insights from spatial-temporal neuroimaging

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Attentional orienting and response inhibition have largely been studied separately. Each has yielded important findings, but controversy remains concerning whether they share any neurocognitive processes. These conflicting findings may originate from two issues: (1) at the cognitive level, attentional orienting and response inhibition are typically studied in isolation; and (2) at the technological level, a single neuroimaging method is typically used to study these processes. This article reviews recent achievements in both spatial and temporal neuroimaging, emphasizing the relationship between attentional orienting and response inhibition. We suggest that coordinated engagement, both top-down and bottom-up, serves as a common neural mechanism underlying these two cognitive processes. In addition, the right ventrolateral prefrontal cortex may play a major role in their harmonious operation.

Keywords: attentional orienting; response inhibition; bottom-up driven; top-down control; event-related potentials; functional magnetic resonance imaging

Introduction

The flexibility and adaptability of human behavior fundamentally rely on executive functions, such as the inhibition of a prepotent response and the selection between response alternatives. These abilities harmonize the relationship between thought and action, and promote higher cognitive processes, such as planning and decision-making. It is widely believed that orienting attention to target locations improves executive function^[1]. Attentional orienting plays a primary role in psychological functions that dynamically direct and optimize perception and actions. With attentional orienting, limited cognitive resources are focused on the information related to the current task. This focus occurs because attentional orienting enhances the representation of the relevant locations or features while inhibiting the irrelevant information in the environment.

This selectivity influences response performance. The engagement of these processes directly leads to increased behavioral sensitivity and decreased response delays and has cognitive benefits.

Both attentional orienting and response inhibition largely affect human perception of the world and adaptation to changing conditions. Understanding the neural mechanisms of both attentional orienting and response inhibition may provide novel insights into attentional and inhibitory pathology in psychiatric conditions (such as attention deficit/hyperactivity disorder). Therefore, it is important to explore under what conditions these processes occur and how they affect performance. However, attentional orienting and response inhibition are traditionally viewed as distinct cognitive domains. Some studies suggest that their neural constructs often overlap, whereas others show the involvement of different brain regions^[2, 3].

To date, no consensus has been reached on whether the two operate independently and why they represent different cognitive processes but activate similar neural structures.

Here we first review the similar neural activations in the networks underlying the two cognitive processes and the evidence from recent human neuroimaging studies using functional magnetic resonance imaging (fMRI). Then, to illustrate that the difference between response inhibition and attentional orienting may depend on different temporal dynamics, neurophysiological investigations into the time-course of activations using the complementary contributions of fMRI and/or electroencephalogram (EEG), are discussed. Finally, the relationship between attentional orienting and response inhibition within a signal task is discussed. Overall, the data suggest that the coordinated engagement of both top-down control and bottom-up driven processes serves as a common neural mechanism underlying the two cognitive operations.

Similarities in the Brain Networks Underlying Response Inhibition and Attentional Orienting

Response Inhibition and Inhibitory Networks

Response inhibition is defined using complex concepts of cognitive control and is required at several levels of processing^[4, 5]. In this review, we focus on the most overt expression of inhibition to stop or interrupt a motor response. From this perspective, response inhibition is the ability to suppress an inappropriate response (tendency to perform an automatic or natural response), avoid interference, and make an appropriate but unnatural response; this ability is essential for flexible responses and efficient adaptation in a dynamic environment. To respond to the task-relevant information and suppress task-irrelevant distractors, goal-directed (or top-down) control is required. This top-down mechanism is assumed to mediate the lower-level sensory and motor areas based on an individual's goal^[6]. Response conflict (the simultaneous activation of incompatible response tendencies) also particularly requires top-down control to inhibit a predominant response in favor of an alternative response or no response at all. Response conflict is thought to be associated with tasks that require the overriding of prepotent responses (response override), require selection from among a set of equally permissible responses

(underdetermined responding), or involve the commission of errors (error commission)^[7–9].

Two types of experimental paradigms, the Go/Nogo task and Stop-Signal task (SST), are usually used to investigate response inhibition. In a Go/Nogo task (Fig. 1A, bottom), only one stimulus, either Go or Nogo, is presented during each trial. Participants are required to perform speeded responses on the Go trials and to withhold their response on the Nogo trials. In an SST (Fig. 1A, top), a stop signal is always presented after a Go stimulus using varying stimulus onset asynchronies (SOAs) for each trial. The participant first makes a motor preparation according to an initial stimulus, then responds when no Stop signal appears or withholds the response when a Stop signal is presented^[2, 3, 10].

The inhibitory network (Fig. 1C, D), related to the cognitive control process, includes the dorsolateral prefrontal cortex (DLPFC), inferior frontal junction (IFJ), inferior frontal gyrus (IFG), anterior insular cortex (INS), dorsal pre-motor cortex, posterior parietal cortex (PPC), anterior cingulate cortex (ACC), and pre-supplementary motor area (pre-SMA)^[11–13]. In particular, two broad regions of the prefrontal cortex, the right inferior frontal cortex (IFC) and the dorsomedial frontal cortex (pre-SMA), are thought to participate in response inhibition^[14]. Several subcortical regions (the subthalamic nucleus, STN^[15] and striatum^[16, 17] in the basal ganglia) may also play important roles in inhibition.

The medial frontal regions, extending to the pre-SMA, have been linked to executive control, such as the control of voluntary action^[18, 19] as well as response conflict^[20]. Studies using Go/Nogo tasks suggest that the ACC is not directly involved in response inhibition but in monitoring conflict^[8, 21, 22].

The SMA is thought to play an important role in the preparation and organization of voluntary movements^[23, 24]. The role of the dorsal prefrontal cortex is still under debate; some have suggested that its function in regards to attention is action selection, but this region does not play a special role in the generation of internally-initiated actions^[18]. In addition, the DLPFC is implicated in working-memory processes^[25], which are required in most selection tasks.

Some neuroimaging studies have suggested that the right IFG is involved in stopping trials^[4, 16, 26]. In the SST,

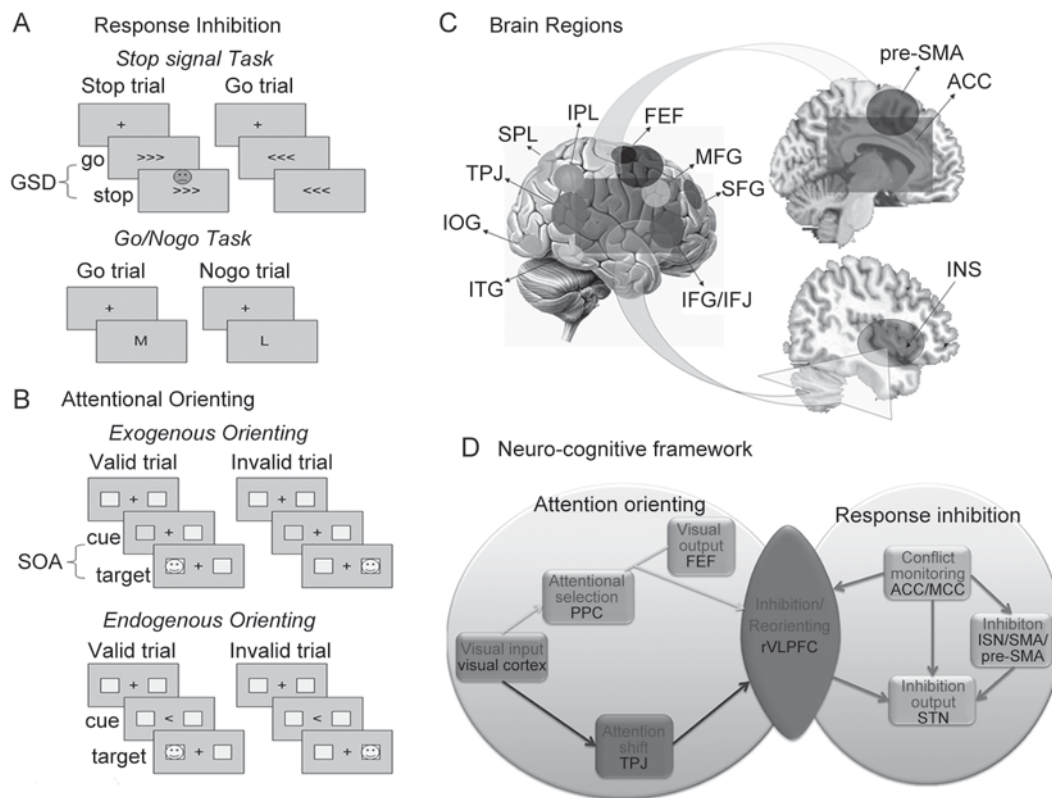


Fig. 1. Experimental paradigms, brain regions, and neuro-cognitive framework. **A:** Experimental paradigms to investigate response inhibition. In the Go/Nogo task (lower panel), a series of Go and Nogo stimuli are presented. In the Go trial, a Go stimulus (M) appears and the participant must press a button to respond. In the Nogo trial, a Nogo stimulus (L) appears and the participant must withhold the response. This measures the ability to withdraw a prepared response. In the SST (upper panel), two kinds of signals are present randomly. In the Go trial, only a Go signal appears (either left or right arrows), and the participant must respond to it. In the Stop trial, a Stop signal (a sad face) following a Go signal is presented and the participant should withhold the response. The interval between Go and Stop signals varies according to the participant's response, and is called the Go-Stop delay (GSD). The Stop signal reaction-time is then obtained to estimate how long it takes to withdraw the prepared motion. **B:** Experimental paradigms to investigate attentional orienting. The exogenous orienting task (upper panel) involves a cue first (a grey square at one of the two peripheral stimulus locations) and then a target (a smiley face), at varied intervals (SOA). The cue and the target are presented in the same peripheral location in valid trials, but in the opposite location in invalid trials. The behavioral index is that the subject responds faster to the target in valid than in invalid trials at short SOAs (<250 ms; facilitation), and slower to the target in valid than in invalid trials at long SOAs (>250 ms; inhibition of return). In endogenous orienting (lower panel), the cue is a centered symbol (an arrow pointing either left or right), and the target is a smiley face. In valid trials, the target is presented in the peripheral location where the arrow pointed. But in invalid trials, the target is presented in the opposite location with regard to the arrow. The behavioral index is that the participant consistently responds faster to the target in valid than in invalid trials, regardless of long or short SOAs. **C:** The main regions related to attentional orienting and response inhibition. **D:** Neuro-cognitive framework. Each block contains an anatomical region below and its functions above. This framework includes attentional orienting-related networks (in the left circle), response inhibition-related networks (in the right circle), and interaction between attention orienting and response inhibition (right ventrolateral prefrontal cortex, rVLPFC). In attentional orienting, light-grey arrows indicate the dorsal network and bold arrows indicate the ventral network. The dorsal network, which includes visual cortex (Fus/MT+/ITG/IOG), PPC (IPS/SPL) and FEF, coordinates endogenous and exogenous orienting, while the ventral network, which includes TPJ (IPL/STG) and rVLPFC (IFG/IFJ/MFG), is activated when attention is reoriented to an unexpected but behaviorally-relevant stimulus. In response inhibition, dark-grey arrows indicate the inhibitory network, which includes pre-SMA, ACC/MCC/INS, STN, and rVLPFC (IFG/IFJ). ACC, anterior cingulate cortex; FEF, frontal eye field; Fus, fusiform cortex; IFG, inferior frontal gyrus; IFJ, inferior frontal junction; INS, anterior insular cortex; IPS, intraparietal sulcus; MFG, middle frontal gyrus; MT+, middle temporal complex; PPC, posterior parietal cortex; pre-SMA, pre-supplementary motor area; TPJ, temporoparietal junction.

this region is activated in both successful and unsuccessful stopping trials but not in no-Stop-signal trials; the activation strength of the right IFG is negatively correlated with the stop signal reaction time (SSRT) in successful stopping trials^[15, 16]. The pre-SMA is also activated in successful stopping trials without any correlation between the activation strength and the SSRT. These findings indicate that the right IFG contributes to response inhibition but not conflict monitoring, whereas the pre-SMA is involved in monitoring or resolving conflicts; thus the right IFG and the pre-SMA are functionally dissociated during the SST. Therefore, it is concluded that activation of these regions results in inhibitory control of motor output *via* a projection to the STN^[3, 4, 15, 27].

Attentional Orienting and Two Frontoparietal Neural Networks

Attentional orienting is important for rapid and efficient searching of visual environments^[28–30] and is commonly studied using Posner's paradigm (Fig. 1). During these tasks, spatial targets are presented at either a cued location (valid trial) or an uncued location (invalid trial). This process is thought to include endogenous and exogenous orienting mechanisms. Endogenous orienting refers to the purposeful allocation of attentional resources to a predetermined location in space, whereas exogenous orienting is thought to be triggered reflexively and automatically by salient stimuli. Previous studies have explored the different characteristics of the two attentional systems^[31, 32] and their neuronal correlates^[33–35]. For example, endogenous facilitation can be maintained for extended periods, whereas exogenous orienting induces an initial facilitation, followed at longer intervals by slower responses to previously explored or attended locations. The early benefit of exogenous orienting at the cued location (exogenous facilitation) is usually attributed to the capture of attention by a peripheral cue. After this initial capture of attention, it is widely assumed that if no target is then presented, the return of attention to the previously-attended location is subsequently inhibited, leading to the phenomenon termed inhibition of return^[36, 37].

Neuroimaging studies demonstrate that attentional orienting processes are likely to involve two important neural networks (Fig. 1D): a dorsal frontoparietal network and a ventral right frontoparietal network. These networks are separate not only in function but also in anatomy^[38].

The dorsal frontoparietal network, which includes the parietal cortex, frontal eye field (FEF), intraparietal sulcus (IPS), fusiform cortex (Fus), and middle temporal cortex (MT+), is related to endogenous and exogenous orienting^[6, 39–41]. This neural network is recruited for the top-down control of visual attention. In the endogenous orienting paradigm (Fig. 1B), a cue elicits transient activation of the occipital cortex (e.g., Fus and MT+), indicating the first sensory process in response to the cue stimulus. In addition, there is sustained activation in the IPS and the FEF in response to the cue, indicating the endogenous attention component in this response (i.e., the arrow, which is not directly related to either the target or the location of the target; instead, it provides the information that prompts participants to allot attention to the peripheral location where the target will appear). Neuroimaging studies also indicate that the dorsal frontoparietal network is modulated by bottom-up saliency stimuli^[42, 43]. In exogenous orienting, such as searching for and detecting a salient stimulus (a target), the features of the target are uncertain (e.g., a red target with green distractors or a green target with red distractors); regardless of whether the response is covert or overt, activation occurs in the FEF. Similarly, the activation in the IPS is modulated by behaviorally relevant tasks. In the exogenous orienting paradigm, researchers found that an exogenous cue (the highlighted grey square in Fig. 1B) activates the dorsal network, including the IPS and FEF^[44–46]. These effects are consistent with the assumption that this network is related to a sensory process and the top-down information of visual expectancy or goals^[42, 43]. These findings indicate that the dorsal network is modulated by interactions between top-down and bottom-up information to specify the relevant object. In addition, the function of the dorsal network is assumed to link the relevant sensory representations and motor maps^[6, 47].

The right ventral frontoparietal network, including the IFG, the temporoparietal junction (TPJ), and the middle frontal gyrus, is related to reflexive reorienting^[2, 6, 38, 48]. This network is largely lateralized to the right hemisphere, and mainly functions to re-orient attention to behaviorally relevant sensory stimuli. It is activated by the detection of a low-frequency target at an attended location. In previous studies in which the participant's gaze remained centered on the target, regardless of the infrequent change in the stimulus, the sensory modality, or the presence of a

variety of response demands^[21, 49, 50], exogenous orienting did not activate the TPJ. And salient irrelevant distractors influenced the dorsal network but not the ventral network. However, unattended stimuli associated with relevant tasks activated the TPJ. This suggests that the ventral network is activated by reorienting to a salient and behaviorally relevant object^[2, 6, 38, 48], and it might therefore primarily be associated with exogenous orienting. Further, the ventral network is recruited along with the dorsal network during exogenous orienting (stimulus-driven or bottom-up driven). Corbetta *et al.*^[6] suggested that these two networks might function interactively. That is, the ventral network is recruited as an alerting system to detect a behaviorally relevant stimulus, whereas the dorsal network identifies the precise location of the stimulus. In addition, the coordination between the ventral (interrupting and resetting ongoing activity) and the dorsal networks (specialized for selecting stimuli and responses) enables adaptation to a rapidly changing environment^[38].

The posterior parietal regions are involved in these two orienting networks and play an important role. Convergent neuroimaging and neuropsychological evidence suggests that the cognitive functional role of the PPC has two parts^[33, 51]. One is the dorsal regions of the PPC including the SPL and the IPL involved in top-down attentional orienting. For example, activations in these regions are commonly observed when the endogenous cues appear, indicating the endogenous signal shift of attention to particular locations in top-down control^[52]. Alternatively, the role of the dorsal regions of the parietal cortex is the attentional disengagement of endogenous orienting^[53]. The other is the ventral regions of the PPC extending to the TPJ involved in bottom-up attentional orienting. For example, salient events capture attention and induce activations of the ventral parietal regions. In addition, the TPJ is commonly activated by salient and task-relevant exogenous stimuli, indicating exogenous attention reorienting to the particular locations^[54].

The Right VLPFC in Response Inhibition and Reflexive Reorienting

The right VLPFC (rVLPFC) plays a critical role in both response inhibition^[10] and reflexive reorienting^[6, 38], and is thus functionally correlated with both attention and inhibition. Either response conflict or response inhibition can activate the right IFG^[55-59]. The IFG appears to

influence the motor system *via* potentiating inputs to the pre-SMA^[60]. Behaviorally relevant reflexive reorienting also activates the ventral network (right IFG/TPJ), whereas the salient irrelevant stimuli influence the dorsal but not the ventral network^[2, 6, 38, 48]. The functional characteristics of the ventral network (poor response to task-irrelevant objects) help to prevent attentional shifts from interfering with task performance.

Response inhibition and reflexive reorienting have gained much attention in the last decades and have led to an explosion in fMRI research^[2, 61]. However, the limited temporal resolution of fMRI makes it difficult to determine the specific roles of these regions. More importantly, it is difficult to determine whether activation of the rVLPFC in a given task is attributable to the engagement of motor inhibition or the attentional orienting processes. Alternatively, it is possible that the psychological distinction between response inhibition and attentional orienting may not project onto different neural networks. Instead, differences in the dynamic time-courses may be a more fundamental distinction between the systems.

Differences in the Temporal Dynamics of Response Inhibition and Attentional Orienting

Accumulating fMRI evidence has confirmed that some neural networks mentioned above are related to both motor inhibition and attentional orienting^[2, 6, 34, 38-40, 48]. However, the low temporal resolution of fMRI signals has restricted these studies mainly to investigating the time-courses of activities: those with neural cognitive processes that are involved in the capture of attention and the control and deployment of attention to some locations^[34, 62]. Thus, the scalp-recorded electroencephalogram (EEG) and event-related potentials (ERPs) elicited by sensory or cognitive processes are beneficial for revealing the precise timing of brain activity associated with specific mental operations.

Response Related ERPs – N2/P3

As noted above, convergent evidence indicates that the right IFG and pre-SMA are crucial for response inhibition^[4, 63]. However, their specific roles in inhibitory functions are not clear due to the poor temporal resolution of fMRI. Some researchers have suggested that the right IFG contributes to response inhibition but not to response conflict, whereas the pre-SMA is involved in monitoring or

resolving the conflict^[4]. Thus, a key issue is to distinguish the function of the right IFG from that of the SMA/pre-SMA within the neural circuit for inhibitory control. The use of ERPs may help to reveal their roles by establishing the time-courses of their involvement.

Electrophysiologically, a frontocentral negative wave at 200–400 ms (the N2 component) and the following anteriorly-distributed P3 component at 300–600 ms are typically used to investigate the physiological basis of inhibitory control. Both the N2 and P3 components have been interpreted as reflections of inhibitory processes in the frontal cortex^[29, 64–68] and thus are indices of inhibitory mechanisms in the Go/Nogo and SST tasks. However, the underlying functional network is still controversial^[65].

Some researchers proposed that the N2 and P3 components are functionally dissociated^[55–59]. Using combined EEG and fMRI, they compared brain responses related to Go and Stop trials, and found that the N2 is related to response conflicts and the P3 is associated with response inhibition.

The N2 component is suggested to be related to increased efforts for response inhibition and to interrupted preparations for response execution^[69]. This component has been localized in the ACC^[70–72] and the DLPFC^[73]. In addition, using a stepped adjustment of response expectation in a response-cueing task (this experiment included three blocks, and the rate of valid cue trials decreased from 80% to 50% to 20%; but the participants were not informed of the change and were required to respond differentially to two target letters), researchers found that unexpected revisions of the response programs enhanced and delayed the N2 component^[74]. Thus, N2 effects may be related to two aspects: monitoring the conflict between competing response tendencies (when it is localized in the ACC), and inhibiting the inappropriate response (when it is localized in the DLPFC)^[73].

Huster *et al.*^[57] recorded N2/P3 after rare stimuli that demand response suppression in both the Go/Nogo and SST paradigms. The results showed that the left anterior region of the mid-cingulate cortex (MCC) is a major neuronal generator of N2, whereas the mid-cingulate generator of the P3 is located in the right posterior MCC. In that study, they also found that the P3 is associated with motor functions, e.g., the precentral region. Using multimodal imaging with EEG and fMRI, the researchers

further found that the Go-related potential (the N2), related to conflict processing, is associated with a mid-cingulate network. The Stop-related potential (the P3), usually involved in motor and cognitive inhibition, occurs in parts of the basal ganglia, anterior MCC, pre-SMA, and anterior INS^[57, 61, 75].

Attention-related ERPs

Endogenous facilitation, exogenous facilitation, and inhibition of return are important components of attentional orienting^[39]. Facilitation and inhibition of return are the faster and slower responses, respectively, to a peripherally-cued target. In the cue-target paradigm (Fig. 1), facilitation is usually found when the interval between the cue and target stimulus (SOA) is <250 ms, whereas inhibition of return is normally observed when the SOA is >250 ms^[28–30, 76].

The attentional orienting and two related networks (dorsal and ventral) have been discussed above. However, it is not clear how attentional orienting modulates information processing in the brain at various stages. ERPs may help to understand the interaction between endogenous (top-down control) and exogenous (bottom-up processing) reorienting. Furthermore, this may provide insights into how attention orienting modulates the early sensory-related stage (P1/N1) and the late response-related stage (P3). The coordinated engagement of both top-down and bottom-up serves as the neural mechanism underlying these two processing stages.

Early sensory-related ERPs – P1/N1 Attentional orienting modulates both the early sensory-related ERPs, P1/N1^[77–85], and the late response-related ERP, P3^[28–30, 34, 41, 86].

Previous studies have shown an enhanced P1 effect in both endogenous and exogenous orienting at a short SOA interval (50–300 ms), that is, *facilitation*; and a suppressed P1 effect at a long SOA interval (>300 ms), that is, the *inhibition of return effect*. The generators of P1 are in the sensory-related cortex, including the middle occipital and the ventral occipital-temporal regions^[29, 30, 78]. The robustly enhanced N1 effect has also been observed during endogenous orienting^[78, 87], but the exogenous N1 varies across different task conditions. For example, a reduced N1 effect was found for both short^[30, 88] and long SOAs^[29, 30]. In addition, the N1 effects disappeared because of the overlap with P1. N1 arises from multiple generators, such as the intraparietal and temporoparietal areas^[28–30], indicating that the exogenous N1 is modulated by a feedback signal from

higher cortex but not by pure sensory components.

Late response-related ERP – P3 P3 indexes the higher-order stages of information-processing involved in updating working memory^[89, 90], decision making^[91, 92], and executive response^[93]. An enhanced P3 is also found in endogenous orienting but only appears in exogenous orienting when the target is relevant to the behavioral response^[28-30, 86, 94]. In endogenous orienting, P3 is localized to the frontal areas. In exogenous orienting (e.g., reflexive orienting), P3 is localized to the middle frontal gyrus, the IFG, and the medial frontal gyrus^[28, 30]. Hopfinger *et al.*^[34] found that the endogenous P3 is larger than the exogenous P3, indicating that endogenous orienting dominates the processing in attentional orienting at the late stage. That is, when both top-down control and bottom-up processing occur at the late response-related stage, top-down mechanisms dominate this processing stage.

The generators of P3, related to attentional orienting, are distributed in the frontal-parietal regions including the IFG, MFG, and pre-SMA. These regions partially overlap the response-related regions^[90]. Specifically, as shown by fMRI, the IFG activations are involved in the detection of infrequent stimuli^[2], Stroop tasks^[95], behaviorally related reorienting^[6, 38], and response inhibition^[2]. These findings show that activations of the IFG depend on the interaction between goal-directed control and stimulus-driven processes rather than one pure process (either a top-down control or a bottom-up process). Green and McDonald^[96], using electrical neuroimaging (beamformer spatial filtering which is used to reconstruct the anatomical sources of the theta frequency band with endogenous orienting), found that the parietal cortex (IPL and SPL) is activated earlier than the frontal cortex (SFG, MFG, and IFG), indicating that endogenous orienting is not initiated solely by the frontal cortex. Analyzing the neuronal activity (*via* EEG) in the interval between the cue and target stimulus, Tian *et al.*^[30] also found that the processing of exogenous orienting involves interactions between bottom-up processes and top-down control.

In fact, attentional orienting, such as facilitation and inhibition of return, is usually measured by the behavioral reaction time (RT) after performing an execution process. That is, the RT data result from the collaboration between both attentional orienting and execution control. In addition, attentional orienting may affect the performance of

executive control. Therefore, it is important to investigate how these two cognitive processes influence each other during a single task.

Relationship between Response Inhibition and Attentional Orienting: Mutual Impacts within a Single Task

At present, it is unclear how response inhibition and attentional orienting relate to each other within a single task. One possibility is that the VLPFC activity observed during one set of tasks can be explained in terms of other putative control mechanisms. For example, recent studies have demonstrated that response inhibition in stopping tasks is often confounded by the demand for orienting to behaviorally-relevant cues; this orienting response may activate the rVLPFC when Stop is required^[60, 61]. Alternatively, reflexive reorienting tasks might also require motor inhibition. Thus, it is important to test the relationships between response inhibition and attentional orienting within a single task.

Attentional orienting and response inhibition have been simultaneously investigated within a single task, such as the Go/Nogo task^[29, 64] and the Stroop task^[97-100]. In these investigations, the processing of one source of information is interfered with by the presence of another information source, such as a list of color names printed in non-matching colors (e.g., the word “red” printed in blue instead of red). Another example is the flanker task^[101, 102] that uses a set of response inhibition tests in cognitive psychology to assess the ability to suppress responses that are inappropriate in a particular context. For example, the flankers might be arrows pointing either in the same direction as the target (congruent, e.g. <<<<<<) or the opposite directions (incongruent, e.g. <<>><<).

Fan *et al.*^[101] found that the orienting network and the executive network are almost completely separate despite some overlap in just a few regions, such as the left superior frontal gyrus (left Brodmann’s area 6). They also found that activation of the orienting network enhances the power in the gamma frequency band, but the gamma activity is significantly reduced when the target appears after the orienting cue. This finding indicates that attentional orienting can minimize the conflict effect by focusing

attention on the target^[102]. Research showed that the Stroop effect is reduced or eliminated at the validly-cued locations in the long SOA interval because the inhibition of return influences the resolution of Stroop interference^[100]. Further, using Vivas's paradigm, Chen *et al.*^[97] found that the left rostral ACC is an important neuronal interface between pre-response conflict and attentional orienting; in addition, the left DLPFC is an important neuronal interface between response conflict and attentional orienting. In the Go/Nogo task after attentional orienting, Tian *et al.*^[29] showed that the reduced Nogo-N2 in the frontal areas, elicited by a validly-cued target, is associated with response preparation inhibition; furthermore, the enhanced Nogo-P3 in the prefrontal areas, elicited by a validly-cued target, is associated with motor response inhibition.

As noted above, strong activation in the rVLPFC is not observed when testing these two effects within a single task. One possible explanation is that endogenous orienting guides attention and focus to objects and helps to reduce or eliminate the interference from distractors; thus, the cost of response inhibition also declines or is eliminated. An alternative reason is that exogenous reflexive reorienting occurs with a behaviorally irrelevant stimulus, i.e., distractors that do not require a response also cannot activate the rVLPFC^[6, 38]. In contrast, the ACC, related to conflict monitoring, is still activated. These findings indicate that the attentional orienting after cognitive control does not affect conflict monitoring but improves motor output. The activation in the rVLPFC during either attentional orienting or response inhibition may be used to prevent the bottom-up process from dominating in both goal-directed and stimulus-driven processes.

Though a large number of studies have focused on the neural mechanisms of both attentional orienting and response inhibition, there are still some issues to be resolved. One proposal is to map the structural connectivity (fiber tract anatomy from diffusion MRI; dMRI) to test whether regions in the rVLPFC (e.g. IFG) are engaged in both tasks. The VLPFC has a connectivity with the ISN revealed by dMRI^[103]. Using dMRI and fMRI in the SST paradigm, Aron *et al.*^[4] found white-matter tracts connecting the IFC, pre-SMA, and STN (and corresponding to task-response BOLD activations), indicating a “hyperdirect” pathway in performing response inhibition.

In experimental studies of visual perception and attention, direct connections between the IPS and the IFG were found^[104, 105], suggesting that these tracks provide a neural basis for the functional interactions of bottom-up and top-down processes. In addition, the tracts between the IFG and Broca's area in the right hemisphere have different connectivity patterns^[105]. These findings indicate that the relationship between reorienting and response inhibition may be related to an underlying structural connectivity.

Final Remarks

In this article, we have reviewed the response inhibition-related and attentional orienting-related networks, namely the dorsal and ventral networks, from spatial and temporal neuroimaging studies. We argued that the overlap of neural structures with differing cognitive process presentations between response inhibition and attentional orienting may be caused by the different dynamic time-courses in the rVLPFC. N2 localized in the ACC shows conflict monitoring and improves motor output when it is activated by attentional orienting after cognitive control, while the attention-related P3 overlaps the response-related regions, especially in the VLPFC, and may be engaged in preventing the stimulus-driven process from dominating in both top-down control and bottom-up processes. Therefore, the coordination with bottom-up driven and top-down control processes serves as the common neural mechanism for these cognitive processes.

To reveal the dissociations and interactions between response inhibition and attentional orienting, functional connectivity may be used to explore the neuronal basis of functional networks. By this method, the overlap in fMRI activations may share populations of neurons across tasks. In other words, an underlying structural connectivity is related to the observed functional connections. In the future, genuine temporal information from the ERP should be read from a scalp potential with a reference at infinity (i.e., zero reference)^[106, 107]. If we knew either the true timing of activation at its actual position or a functional network pattern of the cognitive processing that occurs for both attentional orienting and executive control, the story would almost be complete, and new avenues of research would arise. Certainly, the combination of fMRI, dMRI, and EEG methods would provide important information on the timing

and causal interactions between neural regions^[108, 109].

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