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A common neural hub resolves syntactic and non-syntactic conflict through cooperation with task-specific networks

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ABSTRACT

Regions within the left inferior frontal gyrus (LIFG) have simultaneously been implicated in syntactic processing and cognitive control. Accounts attempting to unify LIFG's function hypothesize that, during comprehension, cognitive control resolves conflict between incompatible representations of sentence meaning. Some studies demonstrate co-localized activity within LIFG for syntactic and non-syntactic conflict resolution, suggesting domain-generality, but others show non-overlapping activity, suggesting domain-specific cognitive control and/or regions that respond uniquely to syntax. We propose however that examining exclusive activation sites for certain contrasts creates a false dichotomy: both domain-general and domain-specific neural machinery must coordinate to facilitate conflict resolution across domains. Here, subjects completed four diverse tasks involving conflict —one syntactic, three non-syntactic— while undergoing fMRI. Though LIFG consistently activated within individuals during conflict processing, functional connectivity analyses revealed task-specific coordination with distinct brain networks. Thus, LIFG may function as a conflict-resolution "hub" that cooperates with specialized neural systems according to information content.

1. Introduction

People face a steady barrage of information throughout the day from various sources of input that threaten to overtake our focus: an incoming text message disrupts our work; an unexpected road closure on a usual route forces re-direction; a background conversation can be hard to ignore. Our attention derails occasionally when competing input contains alluring information that tempts us to rethink our initial plans, actions, or interpretations. However, much of the time, cognitive control procedures allow us to avoid doing something irrelevant or inappropriate to the current situation, by reining in initial reactions to evidential cues that might conflict with goal-relevant processes. For example, we can resist greeting a friend's doppelgänger on the street, even though he or she resembles someone we know well and may evoke strong emotions. We can also avoid coming to the wrong interpretation of Groucho Marx's famous quip—"One morning I shot an elephant in my pajamas"—even though the syntactic ambiguity summons the comical mental image of a giant animal wearing a nightgown.

In this paper, we are interested in how cognitive control mechanisms contribute to sentence processing and the neurobiological systems that support this relationship. As intimated in the prior example, some researchers have hypothesized that one important cognitive control function may be to resolve incompatible representations of sentence meaning that arise due to the incremental nature of comprehension (Novick, Trueswell, & Thompson-Schill, 2005; Nozari, Mirman, & Thompson-Schill, 2016; see also Kaan & Swaab, 2002). Specifically, the control procedures that operate over syntactic material may be general-purpose in nature, engaging the same prefrontal brain systems that detect and resolve information-conflict in other domains such as recognition memory, when familiar-but-irrelevant memoranda interfere with target

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identification (as in the doppelgänger example above; Jonides & Nee, 2006; Nee, Jonides, & Berman, 2007). The evidence for such interplay comes from studies demonstrating co-localized brain activity during syntactic and non-syntactic cognitive control (January, Trueswell, & Thompson-Schill, 2009; van de Meerendonk, Rueschemeyer, & Kolk, 2013; Ye & Zhou, 2009). However, others have argued that language is cognitively and thus neurobiologically distinctive, evidenced by findings of unique activation sites in the same regions for syntactic versus non-syntactic contrasts (e.g., Ben-Shachar, Hendler, Kahn, Ben-Bashat, & Grodzinsky, 2003; Blank, Kanwisher, & Fedorenko, 2014; Embick, Marantz, Miyashita, O'Neil, & Sakai, 2000; Grodzinsky, 2000).

Here, we argue that these discrepancies may lie partly in functional-anatomical assumptions: Prior research on cognitive control has focused on whether one region or a unique set of regions commonly engages to resolve conflict broadly, or whether separate brain areas distinctly support conflict-control functions depending on information content. A similar method is common in the literature on the neurobiology of language, testing whether syntactic processing recruits specialized regions. We propose that overall, this approach creates a false dichotomy: both domain-general and domain-specific neural machinery must coordinate to facilitate complex cognitive processes, in both syntactic *and* non-syntactic domains, because some task demands are shared whereas others are not. The current research therefore circumvents notions about *either* domain-general procedures *or* domain-specific ones; rather, we adopt a network perspective in which cognitive control is accomplished efficiently via functional coupling with separate task-specific regions. That is, a domain-general cognitive-control 'hub' necessarily integrates activity from distributed, domain-specific systems depending on information content (e.g., van den Heuvel & Sporns, 2013).

We test how ostensibly different cognitive tasks theoretically share conflict-control demands with sentence processing and therefore recruit shared neurobiological mechanisms to resolve competitive interactions generally. By itself, this is not a new pursuit. Several prior studies have investigated this issue through tests of co-localized activity, arguing for domain-generality when overlap is observed and for domain-specificity when it is not (cf. Fedorenko, Duncan, & Kanwisher, 2012; January et al., 2009; Ye & Zhou, 2009). Our study is a novel expansion of this approach because it is designed to promote an integrative account, namely how domain-specific (here, syntactic versus non-syntactic) processes coalesce around a domain-general cognitive-control hub when representational conflict arises (Cole, Yarkoni, Repovs, Anticevic, & Braver, 2012). This approach is appealing because of its connection to models in which cognitive-control functions hinge on brief but necessary cooperation with distinct neural systems depending on task content (Cocchi, Zalesky, Fornito, & Mattingley, 2013). Interestingly, in the domain of language processing, resolving conflict during sentence production and comprehension recruits shared control mechanisms in ventrolateral prefrontal cortex (VLPFC) but distinct functional networks that are determined by task type (Humphreys & Gennari, 2014). This suggests cooperation from both domain-general and domain-specific procedures during language processing. Still unknown though is how such functional interconnectivity is modulated across syntactic and non-syntactic domains and whether the same cognitive control hub in VLPFC orchestrates this modulation.

We begin by reviewing evidence for domain-general cognitive control mechanisms that are supported by shared regions within VLPFC. We then turn to theoretical views about whether or not these mechanisms also influence syntactic processing, discussing evidence from both behavioral and neuroimaging experiments. Finally, we present our study, which tests for a general-purpose cognitive-control hub that resolves conflict across syntactic and non-syntactic domains, but forms discrepant networks depending on idiosyncratic task characteristics.

1.1. VLPFC and domain-general cognitive control

It is widely believed that, when dealing with competing stimulus representations, people dynamically adjust their information-processing strategies to comply with current goals or situation-specific demands, by biasing attention only to what is relevant and important to the task (Baddeley, 1996; Barkley, 2001; Friedman & Miyake, 2004; Miyake, 2000; Norman & Shallice, 1986). Prior research has demonstrated that control mechanisms mediate these behavioral adjustments in stages, first by monitoring for and detecting the conflict, and then by deploying cognitive filters to resist or override the distraction (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Derrfuss, Brass, & Yves von Cramon, 2004; Desimone & Duncan, 1995; Miller & Cohen, 2001; Shimamura, 2000; van Veen & Carter, 2006). These findings have offered important insights into how we regulate our thoughts and actions in novel contexts. However, the topic of cognitive control broaches a perennial debate in cognitive science, namely whether the psychological and neurobiological mechanisms that detect and resolve conflict are broad or narrow in scope. Specifically, the problem hinges on whether common procedures filter competing input over a range of cognitive domains to help us avoid mental disruptions in general (Botvinick et al., 2001; Miller & Cohen, 2001; Nee et al., 2007; Rajah, Ames, & D'Esposito, 2008), or whether there are many non-overlapping systems customized to locally support conflict resolution for only certain types of tasks and stimuli (Akçay & Hazeltine, 2011; Egner, Delano, & Hirsch, 2007).

Previous neuroimaging studies do provide some answers to the domain-generality question, but the evidence is mixed. Some findings demonstrate that the same regions within VLPFC, particularly the posterior left inferior frontal gyrus (LIFG), routinely activate under conditions of conflict across a variety of tasks, including recognition memory (Milham et al., 2001; Nelson, Reuter-Lorenz, Sylvester, Jonides, & Smith, 2003) and temporal context retrieval (Rajah et al., 2008). Similarly, other investigations of cognitive control during syntactic processing have observed shared neurobiological recruitment when people encounter different types of conflict, implying that both processing components and overlapping neural substrates are commonly used within individuals to resolve conflict across various kinds of linguistic and nonlinguistic tasks (Humphreys & Gennari, 2014; January et al., 2009; Novick, Kan, Trueswell, & Thompson-Schill, 2009; van de Meerendonk et al., 2013; Ye & Zhou, 2009). This consistent overlap in neural recruitment raises the possibility that these ventrolateral prefrontal areas are multifunctional, reflecting common neurobiological underpinnings that execute domain-general conflict-resolution procedures, including during syntactic processing.

1.2. Domain-general cognitive control contributions to language processing: Evidence for and against

Despite consistency in the findings described above, other evidence shows divisions within VLPFC that are organized by particular mental functions like high-level language processing, suggesting specialized neural tissue dedicated to tasks that are uniquely human and specifically tied to our evolutionary line (Fedorenko, Behr, & Kanwisher, 2011). Within ventrolateral portions of the prefrontal cortex, some of these domain-specific, linguistic areas lie adjacent to domain-general ones, intimating a discrepancy in what processing components are "shared" across tasks (Fedorenko et al., 2012). These functional-anatomical