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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.

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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 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 pre-frontal 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 separations do provide compelling evidence for linguistic modules in the brain, but they still do not preclude the possibility that some language tasks that rely on these processing modules periodically require contributions from other, domain-general cognitive systems.

For example, one way to identify regions involved selectively in high-level language processing is to compare simple sentences to length-matched non-word lists, and then test whether basic sentence comprehension recruits brain regions that are separate from those that come online while completing tasks involving an array of other cognitive challenges, including ones requiring conflict resolution (Fedorenko, 2014). This is a useful approach for testing questions about functional-anatomical specialization for basic language processing (when the sentences are relatively undemanding). Indeed, several studies have shown that

understanding simple sentences generates neural activity that does not overlap with neural activity during a wide variety of nonlinguistic cognitive tasks, suggesting partial separation between basic language processing and broader cognitive functions (see Fedorenko, 2014 for review). However, simple sentence stimuli may not produce certain kinds of processing demands that are often involved in language comprehension. As noted earlier, one important conflict-resolution function during language processing may be to override misinterpretations of syntactically ambiguous input, when the need arises to resolve among incompatible representations of sentence meaning. In the current work therefore, we are interested in *common* cognitive processes across linguistic and non-linguistic domains that might recruit a shared brain region.

A range of behavioral and neurobiological data support this approach: for example, patients with damage to the LIFG, who show deficits in cognitive control (Hamilton & Martin, 2005; Thompson-Schill et al., 2002), also fail to recover from initial misinterpretations during language comprehension (Novick et al., 2009; Vuong & Martin, 2011). Young children demonstrate similar challenges revising syntactic misanalyses (Huang, Zheng, Meng, & Snedeker, 2013; Trueswell, Sekerina, Hill, & Logrip, 1999; Weighall, 2008), which may be linked to protracted cognitive control development (Mazuka, Jincho, & Oishi, 2009; Novick et al., 2005; Woodard, Pozzan, & Trueswell, 2016). And, as sketched earlier, neuroimaging findings show co-localization of activity within the LIFG when the same subjects perform a canonical cognitive control task (Stroop, Flanker) and a sentence-processing task involving syntactic conflict (January et al., 2009; van de Meerendonk et al., 2013; Ye & Zhou, 2009). These correlational findings have been bolstered by recent work demonstrating a *causal* connection between cognitive control procedures and language processing: extensive practice on a cognitive control tasks leads to improved garden-path recovery (Hussey et al., 2016; Novick, Hussey, Teubner-Rhodes, Harbison, & Bunting, 2014); transcranial direct current stimulation of VLPFC mitigates the effects of syntactic ambiguity during real-time processing (Hussey, Ward, Christianson, & Kramer, 2015); and dynamic cognitive control engagement immediately facilitates recovery from misinterpretation during online comprehension (Hsu & Novick, 2016).

Other researchers however have failed to find a link between cognitive control and sentence processing. For example, as described above, the *lack* of overlapping brain regions recruited during cognitive control and high-level linguistic processing might suggest separability of the processing components across tasks (Fedorenko et al., 2012). In the behavioral domain, some findings suggest no correlated variation in performance between cognitive control and syntactic ambiguity resolution (Engelhardt, Nigg, & Ferreira, 2016; Vuong & Martin, 2014). Engelhardt et al. (2016) found that performance on a Stroop-inhibition task did not share unique variance with syntactic ambiguity resolution when accounting for other cognitive factors. Vuong and Martin (2014) found a correlation between garden-path recovery and verbal Stroop performance, but not non-verbal Stroop performance, which suggests a role for domain-*specific*, verbally mediated cognitive control in sentence comprehension. Finally, in language production, Acheson and Hagoort (2014) failed to find a cross-task correlation between an ERP signature of conflict (the error-related negativity, or ERN) during the Flanker task and a speech production task, which the authors interpreted as evidence for distinct cognitive control systems that handle linguistic versus non-linguistic conflict.

Here, we suggest that, by itself, an absence of correlations between syntactic and non-syntactic measures of cognitive control, in both brain and behavior, may not necessarily refute domain-generality, but may instead reflect different conflict-control demands per task. We elaborate on these points in the following section.

2. The current study: Experimental preliminaries and predictions

In the current study, we administer four different conflict resolution tasks, all of which contain verbal material but only one of which involves processing syntactic material. We predict that the different conflict conditions from each task will activate the LIFG within individual subjects because of shared cognitive control demands. However, despite such co-localization, the *degree* of LIFG activity across tasks may not correlate substantially. On the surface, one might expect a domain-general conflict-resolution mechanism to yield correlated variation in behavior or activation levels in the LIFG during conflict conditions in various tasks. However, the expectation of correlations assumes that the strength of the conflict signal (relative to a baseline no-conflict condition) is comparable in magnitude across tasks (e.g., the same degree of elevated reaction times, or increased LIFG activity, etc. in response to conflict). But even if an individual's cognitive control ability is matched in syntactic and non-syntactic domains, the quality and strength of representations that various tasks generate is likely not matched. Representational conflict in one task may therefore be unequal in intensity to representational conflict in another, which would give rise to differences in how strong the need for cognitive control is (and therefore differences in elevated reaction times or LIFG recruitment relative to baseline). Indeed, previous work on executive function frequently finds weak inter-task correlations even *within* a domain, e.g., among tasks of inhibition, although they contribute to the same latent construct (Miyake & Friedman, 2004; Unsworth, 2010). Hence, even though conflict resolution via cognitive control may be consistently needed, there may be no cross-task correlations because task-specific representations are not affected to the same degree (Nozari, Dell, & Schwartz, 2011). While a domain-general cognitive control system therefore expects LIFG recruitment as a conflict-resolution "marker" in any task, it does not necessarily predict correlated variation in the extent of LIFG activity (or behavioral performance). Thus, if we observe within-subject co-localization for the conflict contrasts across four diverse tasks, but not cross-task correlations in LIFG magnitude, we would be hesitant to interpret this null result as evidence for domain-specific cognitive control per se.

Yet there is of course a role for domain-specificity in our approach. Resolving conflict through cognitive control is a process that operates on representations, and the representations that people develop in any given task can *themselves* be domain-specific (e.g., visual and verbal information differ in stimulus characteristics, the sensory-motor organs that handle them, and the cortical regions that store them). As will become evident below, the tasks we administer will require the development of task-specific representations (e.g., syntactic vs. non-syntactic), even if the *process* of resolving conflict among incompatible representations in each task is common and may thus be domain-general. Therefore, we expect functionally specialized neural networks to couple with LIFG to show task-dependent connectivity. Under this scenario, a domain-general cognitive control hub within LIFG resolves conflict during syntactic and non-syntactic tasks alike, but there is

diversity in the amount of control recruited based on an individual task's needs (due to differences in the type and strength of representations that each task generates).

Thus, these ideas lead us to test the following specific predictions. First, conflict resolution —independent of information content—will recruit a domain-general hub, namely, regions within the LIFG given their canonical response to conflict processing during syntactic and non-syntactic tasks in both neuroimaging and neuropsychological studies (January et al., 2009; Jonides & Nee, 2006; Nelson, Reuter-Lorenz, Persson, Sylvester, & Jonides, 2009; Smith & Jonides, 1999; Ye & Zhou, 2009). To account for variability across individuals in brain size, morphology, and region location (Amunts et al., 1999; Tomaiuolo et al., 1999), we take a fine-grained, single-subject approach to best determine what exactly is shared across tasks, providing a clearer picture of functional-anatomical specificity than what group-level analyses can reveal (Derrfuss, Brass, von Cramon, Lohmann, & Amunts, 2009; Derrfuss & Mar, 2009; Fedorenko, Hsieh, Nieto-Castanon, Whitfield-Gabrieli, & Kanwisher, 2010; Fedorenko & Kanwisher, 2009; Fedorenko, Nieto-Castañón, & Kanwisher, 2012; Nieto-Castañón & Fedorenko, 2012). Second, other brain regions may come on-line depending on task-specific information content and how much control is needed to resolve conflict in that particular task. That is, we assume that localization approaches alone are insufficient to gain a comprehensive picture of neural dynamics; rather, brain regions form networks to communicate rather than act in isolation (Bassett et al., 2011; Cole et al., 2013; Friston, 2011; Hutchison et al., 2013; Mesulam, 1990). Specifically, other regions may dynamically interact with domain-general ones in order to meet task-specific requirements. It is reasonable to assume that resolving conflict involves domain-general procedures (e.g., a shared brain region that activates during a range of cognitive control tasks) but, in addition, it might require co-activating a domain-specific network, e.g., a set of neural areas that engage under some but not all conditions, depending on task demands and the representations being processed (Fedorenko & Thompson-Schill, 2014; Hsu, Novick, & Jaeggi, 2014). The presence of both activation patterns would suggest a cognitive-control hub around which task-specific networks interact on the basis of information content and diversity in the extent of conflict resolution demands.

Considering network connectivity, moreover, affords a nuanced look at the underlying neural mechanisms of conflict resolution. Rather than viewing co-localization as evidence in favor of domain-generality, or lack thereof as support for domain-specificity, this approach might reveal that it is both: namely, how a multipurpose cognitive control hub—agnostic to whether the conflict arises from syntactic representations—might cooperate with domain-specific system networks to resolve conflict effectively (van den Heuvel & Sporns, 2013). Here, we examined both broad and specific brain activation across a range of cognitively demanding syntactic and non-syntactic tasks, using posterior LIFG as a candidate region (January et al., 2009; Jonides & Nee, 2006; Smith & Jonides, 1999; Ye & Zhou, 2009). Our anatomically constrained, functional LIFG region (see Section 3.4) partially overlaps with the one used by Humphreys and Gennari (2014), which showed co-activation during language production and comprehension involving conflict. We test whether the boundary condition for this cognitive-control hub extends beyond syntactic lines.

Subjects completed four conflict-control tasks (one syntactic, three non-syntactic) that independently have been well-established to tap the LIFG (Carter, Mintun, & Cohen, 1995; Jonides & Nee, 2006). Each task contained a condition in which people encountered conflicting representations: a memory updating task involving familiar but irrelevant stimuli (Jaeggi, Buschkuehl, Jonides, & Perrig, 2008; Jaeggi, Buschkuehl, Shah, & Jonides, 2014), an item recognition task involving proactive interference (Jonides & Nee, 2006), a sentence comprehension task involving syntactic ambiguity resolution (Christianson, Williams, Zacks, & Ferreira, 2006), and a Stroop task (Carter et al., 1995; Stroop, 1935). Importantly, despite sharing a condition requiring some form of conflict resolution, the tasks differed substantially in terms of their computational demands and stimulus characteristics (see Fig. 1 for the critical conditions of each task). The common recruitment of the LIFG during conflict would provide further evidence for its domain-general role in countermanding cognitive conflict. But we also harness functional connectivity approaches to find meaningful variation across these tasks that may tap into task-specific content in conjunction with domain-general processing mechanisms. Diverse network patterns might manifest depending on memory demands, stimulus characteristics, task goals (e.g., item recognition; sentence comprehension), and thus variability in how strong the representational conflict is and thus how much control is needed. Consequently, we predict co-localization for conflict across tasks in the LIFG, which will "communicate" with unique networks depending on task-specific characteristics.

Finally, we also examined regions of the multiple demand (MD) system—a catalog of frontal and parietal areas that have been shown to engage during a diverse array of cognitive demands including "focused attention, goal maintenance, strategy selection, performance monitoring, and other activities" (Fedorenko, Duncan, & Kanwisher, 2013). That is, the MD system is not specifically recruited for conflict-resolution procedures, but comes online to manage a broad range of cognitive challenges (Cabeza & Nyberg, 2000; Duncan, 2010; Fedorenko et al., 2013). By testing for activity throughout the global MD system in addition to the LIFG, we can evaluate the extent to which LIFG involvement should be ascribed to some broad-range processes that might engage for several kinds of cognitive challenges, or to the engagement of a more specific conflict resolution mechanism per se. We predicted that we would find selective LIFG activation for our conflict contrasts rather than global MD system recruitment.

3. Method

3.1. Subjects

Twenty-eight right-handed subjects (16 men; average age = 22.2 years, range = 18–32 years) were paid for their participation. All subjects were native monolingual speakers of English, were not taking any psychoactive medications, had no history of neurological disorders, had normal or corrected-to-normal vision, and were not color-blind. Subjects provided written informed consent, and the human subjects review board at the University of Maryland approved all experimental procedures.

3.2. Materials and procedure

After a short practice session that occurred 1–2 days prior to the MRI scan, subjects completed the following four tasks while in the scanner.

Item recognition (Recent Probes)—Each trial of the task began with a 500-ms fixation cross, followed by a 2000-ms presentation of an array of four letters that subjects were instructed to remember (e.g., "m k d i"). After a 2500-ms delay interval, they determined whether a probe item matched a letter from the immediately preceding set (e.g., "K"). Half of the stimuli required a match (i.e., "yes") response, and half required a non-match (i.e., "no") response. Conflict was induced on a subset of trials by presenting a recognition probe (e.g., "A") that was not a member of the current memory set (e.g., "t b e f ") but was a member of the memory set on the *previous* trial (e.g., "a m g p"). On these critical "recent-no" trials, subjects must override a familiarity bias to correctly reject the probe as a non-match (Jonides & Nee, 2006; Monsell, 1978). Over the course of three runs, this manipulation yielded four conditions of 30 trials each: recent-yes, recent-no, non-recent-yes, and non-recent-no. The recent-no trials were compared to the non-recent-no trials as the conflict contrast of interest (see Fig. 1). Each trial lasted 7500 ms, and jittered fixation periods lasted anywhere from 0 to 12.5 s between trials.

Memory updating (n-back)—For this task, we selected 144 four-to eight-letter highly familiar English nouns and adjectives that ranged in frequency (12–129), concreteness (249–613), and imageability (334–575) based on values in the MRC Psycholinguistic Database (Wilson, 1987).

Each trial lasted 2500 ms, beginning with a fixation cross that appeared for 150 ms, followed by a single word stimulus appearing on the screen for 2000 ms, and a 350-ms inter-stimulus interval (ISI). Upon presentation of the word stimulus, subjects pressed a button to indicate whether the current word on the screen matched or mismatched the one presented three trials ago (i.e., "3-back"). Subjects completed three runs of the task, and different sets of words were used for each run. Of the 96 trials in each of the three runs, 48 items were targets, 36 were "lures" (words that appeared recently, but not in the 3-back position), and 12 were novel (i.e., non-lures), thereby balancing "match" and "mismatch" responses across items. Non-lures were randomly selected from the same pool of words as targets and lures, wherein any potential orthographic or phonetic overlap with targets was incidental. Of the 36 lures, we included 12 2-back lures, 12 4-back lures, and 12 5-back lures. These items required conflict resolution because subjects must override a familiarity bias to correctly reject the lure as a non-target. This manipulation introduces a type of conflict that is considered similar to that tapped in the Recent Probes task and during syntactic ambiguity resolution (Chatham et al., 2011; Hussey et al., 2016; Novick et al., 2014; Szmalec, Verbruggen, Vandierendonck, & Kemps, 2011). Therefore, the lure trials were compared to the target trials as the conflict contrast of interest (see Fig. 1).

Subjects responded to each trial by button-press, indicating "yes" for the targets and "no" for the lures and non-lures. Jittered fixation periods appeared between trials.

Syntactic ambiguity resolution—For this task, 26 verbs that could be used both transitively and reflexively (e.g., "hid") were drawn from Christianson and colleagues (Christianson et al., 2006) and were used to create 20 ambiguous and 20 unambiguous sentences. For example: "While the thief hid the jewelry that was elegant and expensive sparkled brightly." is temporarily ambiguous as to whether the thief is hiding himself (reflexive) or the jewelry (transitive). Readers reliably adopt the transitive interpretation initially (see Christianson, 2001; Christianson et al., 2006; Novick et al., 2014), but late-arriving input (e.g., "sparkled brightly") requires revision to the reflexive interpretation instead (that the thief was hiding himself while the jewelry sparkled). The unambiguous control condition included a comma ("While the thief hid, the jewelry…"), forcing the reflexive analysis. Crucially, the comma manipulation preserves construction type across conditions, varying only whether the sentence was temporarily ambiguous or not. Therefore, ambiguous sentences were compared to unambiguous sentences as the conflict contrast of interest (see Fig. 1). Verbs that repeated appeared in new sentence contexts. The 40 items were embedded within 80 filler sentences, which did not contain syntactic ambiguities and used a variety of sentence constructions to draw attention away from the ambiguity manipulation in the critical sentences. Ambiguity was manipulated across items, but not within items (i.e., there were not multiple lists that presented ambiguous and unambiguous versions of the same sentence items across subjects).

Comprehension questions were presented after 40% of sentences to keep subjects on task; however, accuracy data are not analyzed here due to the low number of occurrences. Responses were balanced across all 48 probed sentences (8 ambiguous, 8 unambiguous, 32 filler) and across response options (i.e., 24 "yes" and 24 "no" responses).

Each trial began with a 500-ms "Ready" prompt. The entire sentence was then displayed on the screen for 7000 ms. When subjects finished reading the sentence, they pressed a button, which removed the stimulus and prompted a fixation cross to appear. For the 40% of trials that included a comprehension question, a "?" then appeared for 1000 ms, followed by the question. Subjects indicated a "yes" or "no" response via button-press. Regardless of whether or not subjects responded, trials without questions lasted 7500 ms, and trials with comprehension questions lasted 12,500 ms. Jittered fixation periods appeared between trials. There were four runs of the task, with an equal proportion of ambiguous, unambiguous, filler, and trials with comprehension questions balanced across runs. Due to technical errors, one participant did not complete the syntactic ambiguity task.

Stroop—Subjects performed a button-press Stroop color-identification task (borrowed from Hindy, Altmann, Kalenik, & Thompson-Schill, 2012; January et al., 2009; see also Milham et al., 2001). We restricted the possible responses for this task to three colors: blue, yellow, and green. On each trial, subjects saw a single word and were instructed to press the button that corresponded to the font color of that word. Stimuli included incongruent and neutral trials. For incongruent trials, the font color did not match the color word (e.g., "blue" written in yellow ink). To optimize the conflict effect, incongruent trials included both response-ineligible trials (where the color word was not a possible response option, e.g., "orange" in yellow ink) and response-eligible trials (where the color word was a possible response option, e.g., "blue" in yellow ink). Neutral trials did not use color terms (e.g., "farmer",

"tax") and were intermixed with incongruent trials. Incongruent trials (including both response-ineligible and response-eligible trials) were compared to neutral trials as the conflict contrast of interest (see Fig. 1).

Each trial lasted 2.5 s, beginning with a fixation cross that appeared for 450 ms, followed by the Stroop stimulus appearing on the screen for 1800 ms, and a 250-ms ISI. Each block of the Stroop task consisted of 48 trials: 24 neutral trials and 24 incongruent trials. There was a total of four blocks during each of two runs, with 10-s breaks between blocks. During the breaks, subjects were visually reminded of the order of the buttons that corresponded to each ink color.

Because the Stroop task is a canonical cognitive control task, it was our intended "localizer" task for testing subsequent contrasts of interest, in line with previous work (Hindy et al., 2012; January et al., 2009). We therefore presented it last in order to prevent subjects from detecting the experimental manipulations and devising strategies that they might use throughout the session. The other three tasks were presented in a randomized order for each subject to remove order effects. However, to test our domain-generality claim more extensively, we ultimately used each of the other three tasks as a "localizer" as well.

3.3. Image acquisition

We acquired imaging data using a 3T Siemens Trio system with a 32-channel head coil and foam padding to secure the head in position. We initially acquired T1-weighted anatomical images (TR = 1900 ms, TE = 2.32 ms, TI = 900 ms, flip angle = 9.00 degrees, voxel size = 0.4492 mm × 0.4492 mm × 0.900 mm). Then, each subject performed the memory updating, item recognition, sentence comprehension tasks in a randomized order, followed by the Stroop task, all while undergoing blood oxygen dependent (BOLD) imaging (Ogawa et al., 1993). We collected 2129 sets of 40 slices (Stroop: 428; Recent probes: 554; 3-back with lures: 447; Syntactic ambiguity: 700) using interleaved, gradient echo, echoplanar imaging (TR = 2500 ms, TE = 28 ms, flip angle = 70.00 degrees, voxel size = 3.0 mm × 3.0 mm × 3.0 mm). A set of "dummy" gradient and radio frequency pulses preceded each functional scan to allow for steady-state magnetization; no stimuli were presented and no fMRI data were collected during this initial time period.

3.4. Neuroimaging data analysis

We analyzed the data off-line using the FMRIB Software Library (FSL) toolkit (http://www.fmrib.ox.ac.uk/fsl). Anatomical data for each subject were processed using FSL to perform brain extraction (Smith, 2002), correct for spatial intensity variations (Zhang, Brady, & Smith, 2001), perform non-linear noise reduction (Smith & Brady, 1997), and co-register to a standard template in Montreal Neurological Institute (MNI) space. Functional data were sinc interpolated in time to correct for the slice acquisition sequence and motion corrected with a six-parameter, least squares, rigid body realignment routine using the first functional image as a reference. We then also normalized the data to MNI space. The fMRI data were smoothed using a 5 mm full-width half-max (FWHM) Gaussian smoothing kernel. Previous work has shown that smoothing in single-subject analyses does not differ from traditional group analyses with a sufficient sample size (Mikl et al., 2008). We also chose a

modest kernel that would increase sensitivity to the signal of interest while retaining anatomical specificity. Then, following preprocessing for each subject, a power spectrum for one functional run was fit with a 1/frequency function, and this model was used to estimate the intrinsic temporal autocorrelation of the functional data (Zarahn, Aguirre, & D'Esposito, 1997).

We fit a modified general linear model, or GLM (Worsley & Friston, 1995), to each subject's data, in which we modeled the onset and entire duration of each task trial of each condition as a single event, and convolved with a standard hemodynamic response function.[3] From each GLM, we computed parameter estimates for the conflict condition (relative to the no-conflict condition), which were included in group-level random effects analyses.

We identified regions of interest (ROIs) as the single-subject level, because group-level effects might conceal a clean discernment of functional-anatomical specificity or, worse, reveal averaged co-localization that does not actually exist on an individual basis. To account for differences in brain anatomy, we used Free-Surfer's cortical segmentation tool to individually identify LIFG as the union of the pars triangularis and pars opercularis subregions (BA 44/45 in MNI space). As comparison ROIs, we also included the major components of the MD system, as proposed by Duncan (2010). These control ROIs included bilateral middle frontal gyri, anterior cingulate cortex, supplementary motor area (SMA), inferior and superior parietal cortex, precentral gyrus, and insula. We confirmed the adequacy of region delineation through visual inspection. On a subject-by-subject basis we identified the top 100 active voxels during the Stroop task (contrasting conflict and no-conflict trials) within each region, with no constraints on contiguous voxels or on threshold. ROIs could not be identified in three subjects (because there were not sufficient voxels showing more activity for conflict versus no-conflict trials), and those subjects were therefore excluded from subsequent neuroimaging analyses. For the remaining 25 subjects, there was enormous heterogeneity in the resulting individual ROIs (see Fig. S1). We repeated this procedure iteratively, using each of the other three tasks as a "localizer." Within each anatomically constrained functional ROI, we then calculated parameter estimates for each subject on the spatially averaged time series across the 100 voxels in the ROI, using these estimates to assess conflict effects (relative to conditions without conflict) across the three other tasks. We used a one-sample *t*-test to assess the group-averaged conflict effect relative to zero.

For functional connectivity network analyses, we used psychophysiological interaction (PPI) analyses to examine functionally connected networks of brain regions that co-engaged with LIFG. Specifically, we tested our prediction that the LIFG serves as a con-flict resolution "hub" around which distinct networks are recruited depending on information content and cognitive control demands. We conducted PPI analyses in FSL (O'Reilly, Woolrich, Behrens, Smith, & Johansen-Berg, 2012), using each subject's anatomical LIFG ROI as the seed region.[4] The physiological variable was the average time course of activity in the LIFG

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[3]While three of the tasks contained an equal number of trials for the conflict and no-conflict conditions, the design of the memory updating task led to more target (144) than lure (108) items. Note that this imbalance does not impact the estimated BOLD effect size – it does make the contrast between the two conditions more uncertain because of the difference in the number of items included, but the comparison remains valid.

seed region for each subject. The psychological variable was the conflict contrast for each task (conflict > no-conflict). This variable was convolved with the gamma function, and temporal derivatives with temporal filtering were added. The PPI regressor was defined as the interaction term between the zero-centered psychological regressor and the demeaned physiological regressor. After conducting single-subject analyses as the first level, we raised these to a second-level group analysis using a threshold of at least 10 contiguous voxels and $t = 3.09$ ($p < 0.001$, uncorrected).

4. Results

4.1. Behavioral conflict effects

We first analyzed the data from each of the three tasks to determine the impact of information-conflict on behavior (reminder: because only 40% of the sentences in the syntactic ambiguity task included a comprehension question, we did not analyze behavioral data from that task).

Item recognition (Recent Probes)—Repeated-measures ANOVAs revealed a significant recency (recent vs. non-recent) X response (yes vs. no) interaction on both error rate (ER: $F[3,81] = 7.50$, $p < 0.001$) and RT ($F[3,81] = 6.77$, $p < 0.001$). We probed this interaction by comparing conflict (recent-no, RN) trials relative to no-conflict (non-recent-no, NRN) trials, which were of primary interest. Paired-sample, two-tailed t-tests (used for all subsequent tests) demonstrated that subjects committed reliably more errors (RN: M = 10.00%, SE = 2.33%; NRN: M = 6.45%, SE = 2.02%; $t[27] = 4.19$, $p < 0.001$) and were significantly slower to respond correctly (average median RT: RN: M = 907 ms, SE = 42 ms; NRN: M = 832 ms, SE = 35 ms; $t[27] = 4.63$, $p < 0.001$) on RN vs. NRN trial types. These patterns reflect the standard conflict effect for this task. As expected, recency did not affect 'yes' responses in error rate ($t[27] = 1.58$, $p = 0.13$) or in response time ($t[27] = 0.38$, $p = 0.71$).

Memory updating (n-back)—Repeated-measures ANOVAs revealed significant effects of trial type (lures, targets, novel items) on both accuracy ($F[2,54] = 17.99$, $p < 0.001$) and response time (RT: $F[2,54] = 32.20$, $p < 0.001$; see Supplemental Text). Although subjects did not differ in accuracy to memory lures (M = 73.9%, SE = 3.0%) relative to targets (M = 74.5%, SE = 3.0%; $t[27] = -0.17$, $p = 0.87$), they were significantly slower to respond correctly to lures (average median RT: M = 1040 ms, SE = 36 ms) than targets (average median RT: M = 826 ms, SE = 35 ms; $t[27] = 8.36$, $p < 0.001$).

Stroop—Subjects demonstrated fairly low Stroop ERs across all trial types (Incongruent: M = 6.53%, SE = 1.73%; Neutral: M = 6.14%, SE = 1.96%), so there was no reliable

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[4]Although we have argued for preserving individual differences in neuroanatomy through the use of single-subject anatomically-constrained functional ROIs, this approach could very well undermine our network analyses. Namely, by identifying ROIs at the individual level both anatomically and functionally, but averaging our network analyses at the group level (in order to identify the most active regions covarying with LIFG during each task), it may be difficult to find group-level network connectivity results that survive threshold. To compromise, we opted for an individually-identified anatomical LIFG ROI (thus foregoing the additional functional constraint, in maintaining some degree of individual specificity), which we report here, but importantly, note that a secondary analysis incorporating the functional constraint revealed similar results.

difference across conditions (t[27] = 0.82, $p > 0.4$). However, on correct trials, subjects were significantly slower to respond to incongruent Stroop items (average median RT = 611 ms, SE = 17 ms) versus neutral trials (average median RT = 582 ms, SE = 16 ms; t[27] = 5.85, $p < 0.001$).

4.2. ROI co-localization analyses

We turn now to the fMRI data, using single-subject Stroop-identified functional ROIs within LIFG and testing for conflict effects from the other three tasks in this ROI. These results are shown in Fig. 2, which plots the parameter estimates (converted to percent signal change) for the conflict contrast of interest for each task, averaged across subjects. The memory updating, item recognition, and sentence comprehension tasks all showed reliable conflict effects within these Stroop-identified ROIs in 77–88% of subjects, depending on the task (average percent signal change: memory updating, M = 0.11, SE = 0.04, t(25) = 2.95, $p = 0.007$; item recognition, M = 0.05, SE = 0.02, t(24) = 2.37, $p = 0.02$; sentence comprehension, M = 0.12, SE = 0.03, t(25) = 4.45, $p < 0.001$).

Importantly, these co-localization results were consistently found, no matter which task was used as the localizer. For example, when using the lures > target contrast from the memory updating task to localize voxels in an otherwise identical procedure, similar results emerged (Stroop: M = 0.08, SE = 0.02, t(25) = 3.35, $p = 0.003$; item recognition: M = 0.06, SE = 0.02, t(24) = 2.72, $p = 0.01$; sentence comprehension: M = 0.21, SE = 0.03, t(25) = 6.00, $p < 0.001$). Finally, when using the conflict contrast from either the sentence comprehension task or the item recognition task, we found the same pattern (ps < 0.01; Fig. 2). Notably, these effects survived Bonferroni correction for the three additional localizer tests ($p < 0.05/3$ = corrected $p < 0.017$).

Next, to evaluate the specificity of our co-localization finding, we wanted to test whether LIFG involvement could be attributed to broad-range processes that might engage for various cognitive challenges, or whether our finding reflected a more specific conflict-resolution mechanism. Therefore, we conducted the same set of co-localization tests in each of the 16 MD regions, using the conflict contrast from the Stroop task as the functional localizer, just as we did within LIFG. Within each MD region, we performed the same analysis as within LIFG, testing for conflict effects across the other three tasks. As can be seen in Fig. 3, using a Bonferroni-corrected threshold ($p < 0.05/16$ = corrected $p < 0.003$) to account for the multiple statistical tests, no MD regions demonstrated significant conflict effects across the three non-Stroop tasks in the same manner as LIFG did (the full matrix of task activation within MD regions is provided in Table S1). Importantly, because the entire MD system routinely responds to a vast array of complex cognitive challenges (Duncan, 2010), this result indicates that the universal LIFG activity under conditions of increased conflict is unlikely due to task difficulty alone (Fedorenko et al., 2013), but rather to our experimental manipulation of conflict-control demands more specifically (see Section 5.2).

4.3. Correlations in LIFG activity across tasks

As predicted, the data above show that the different conflict conditions from each task routinely activated the posterior LIFG within individual subjects. However, as detailed

earlier (Section 2), our account of a general-purpose conflict-control system does not necessarily expect that the degree of LIFG activity across tasks should reliably correlate alongside strong co-localization findings. There are substantial differences in task properties and representations (e.g., syntactic vs. non-syntactic) that must be processed, leading to differences in the representational quality of the conflict signal (compared to no-conflict) across tasks. Moreover, even tasks within the executive function domain often demonstrate low cross-task correlations (Miyake & Friedman, 2004). Therefore, we expect diversity in how much cognitive control is needed to resolve the conflict in each task, which should generate different levels of LIFG activation per task. Here, using pair-wise correlations with correction for multiple comparisons, we test whether there is a correlation in the degree of LIFG activation in the four tasks across subjects. Our variable of interest was the parameter estimate (converted to percent signal change) in LIFG for each conflict contrast (i.e., the values plotted in Fig. 2).

As can be seen in Table 1, there are no significant correlations in LIFG activity across the four tasks when correcting for multiple comparisons (i.e., a Bonferroni correction for multiple comparisons of $p < 0.05$ over 3 localizer tests means that a correlation coefficient must correspond to $r > 0.45$, $p < 0.017$ in order to surpass corrected threshold and be considered statistically significant). Though some have argued that such a lack of correlated variation reflects domain-specificity (Acheson & Hagoort, 2014; Engelhardt et al., 2016; Vuong & Martin, 2014), we have been arguing that this null pattern does not necessarily indicate support for domain-specificity, particularly in view of our co-localization patterns (see also Miyake & Friedman, 2004; Unsworth, 2010). Rather, a lack of correlated variation in LIFG activity may simply index distinct task demands, differences in information content, and variability in how much conflict each task elicits relative to baseline.

In what follows, we present connectivity data that test network co-engagement with LIFG during conflict processing for each task to illustrate how domain-specific processes do communicate with the domain-general LIFG hub. Note that our goal here is not to claim that recruitment of domain-specific networks *accounts* for the lack of correlations across conflict effects from different tasks. Instead, we intend to show how domain-specific representations and processes *contribute to* a domain-general mechanism that regulates behavior while handling conflict. We show that there are separate sets of brain regions that coordinate with the LIFG that vary on the basis of task specificity, namely diversity in the representations and amount of control recruited for what each task requires. We suggest that such connectivity patterns show how a domain-general cognitive control system interacts with task-specific networks.

4.4. Functional connectivity network analyses

We examined functional connectivity across the whole brain (see Fig. 4 for a representative set of clusters, and Table S2 for the full list of clusters identified for each task), which revealed that distinct combinations of brain regions co-engaged with LIFG depending on task, as reported below. For easy viewing, we also refer the reader to an online video that moves along the axial axis through the whole brain, in which LIFG co-engagement and task-specific interconnectivity with the LIFG can be clearly discerned: http://ter.ps/connectivity.

Stroop—The only region whose co-variation in activity with LIFG surpassed threshold for the conflict contrast (incongruent vs. neutral) was a cluster of voxels in left inferior temporal/occipital fusiform gyrus (MNI coordinates: −54, −62, −24). This area is typically referred to as the "visual word form area" (VWFA) and is linked to word recognition and word meaning (Dehaene & Cohen, 2011).

Item recognition (Recent Probes)—A collection of posterior regions co-engaged with LIFG during item recognition involving conflict (recent-no vs. non-recent-no), including bilateral parahippocampal gyri (−34, −24, −16; 34, −30, −12) and left middle temporal gyrus (−48, −50, 6). The coordination of these regions with LIFG is unsurprising, given the high memory demands of the item recognition task and the interplay of frontal and temporal regions during memory retrieval (Bunge, Burrows, & Wagner, 2004). Frontal regions including the right paracingulate gyrus/anterior cingulate cortex (12, 16, 38) and right subcallosal cortex/frontal orbital cortex (2, 14, −26) were also activated.

Memory updating (n-back)—LIFG activity during lure trials compared to targets co-engaged a set of frontal and parietal brain regions whose profile bears similarity to other studies using the n-back paradigm and particularly those that include lure trials (Gray, Chabris, & Braver, 2003; Owen, McMillan, Laird, & Bullmore, 2005). These regions included superior frontal regions (−18, 22, 48; 14, 8, 66), right motor cortex (4, −8, 48), bilateral intraparietal sulcus/supramarginal gyrus (−34, −40, 36; 54, −42, 36), and right dorsal posterior cingulate (6, −46, 18). Moreover, the memory updating task involved single word stimuli and, like the Stroop task, LIFG activity co-varied with activity in the left inferior temporal gyrus, or the VWFA (−50, −64, −12). Finally, regions involved in the cingulo-opercular network were also engaged during the memory updating task, including medial frontal regions and the frontal operculum. We return to this particular task network profile in Section 5.

Syntactic ambiguity resolution—When comparing ambiguous to unambiguous sentences, LIFG co-engaged with regions including left anterior prefrontal cortex (−30, 54, 6), bilateral cingulate cortex (−10, 22, 38; 2, 16, 50), right middle frontal gyrus (40, 22, 30), right precuneus (12, −56, 56), and left supplementary motor cortex (−6, −4, 78). Together, some of these regions comprise frontal and parietal regions that overlap with much of the language network (see Fedorenko & Thompson-Schill, 2014 for review), but others are distinct from this network for possible reasons that we return to in Section 5.

5. Discussion

Our results are the first to demonstrate that a combination of domain-general and domain-specific neural machinery function collaboratively to resolve conflict. We used a mixture of single-subject co-localization analyses and functional connectivity approaches to illustrate cooperation between the LIFG and task-specific networks during syntactic and non-syntactic conflict processing. There are several novel aspects to our findings. First, cognitive control appears to be a domain-general process that draws on the same neural regions to resolve conflict despite otherwise ostensible differences in the four tasks we administered. The LIFG was recruited consistently to resolve conflict, regardless of whether it was during

language comprehension (e.g., to revise misinterpretations), resolution of proactive interference in memory, or inhibition of a dominant but irrelevant response. Yet LIFG-supported cognitive control communicated with diverse networks while processing conflict depending on task-specific properties. That is, if cognitive control was operating over syntactic representations, the LIFG connected with a network that was distinct from the one formed when cognitive control operated over representations in recognition memory. In what follows, we elaborate on these findings in the context of previous research and discuss their overall implications.

5.1. Connection to prior research

Though a range of prior neuroimaging, behavioral, and patient data suggest that common cognitive control procedures help language users resolve conflict during sentence comprehension (Hsu & Novick, 2016; Humphreys & Gennari, 2014; January et al., 2009; Novick et al., 2005, 2009; van de Meerendonk et al., 2013; Vuong & Martin, 2011; Ye & Zhou, 2009), other data suggest distinctions in the cognitive control systems that operate over syntactic and non-syntactic material, leading to claims of domain-specificity (Acheson & Hagoort, 2014; Engelhardt et al., 2016; Fedorenko et al., 2012; Vuong & Martin, 2014). Our study tested the effects of increased conflict resolution demands across four diverse tasks, one of which involved syntactic conflict and three of which did not. However, rather than adopting a perspective wherein there is influence from *either* domain-general *or* domain-specific systems, we took a network approach, assuming that cognitive control is successfully achieved through functional coupling between domain-general mechanisms that operate in conjunction with task-specific processes. Given the canonical response of posterior LIFG to increased conflict-control demands in both syntactic and non-syntactic contexts, we predicted first that it would commonly engage to resolve conflict across different tasks. This prediction was supported, replicating prior co-localization studies, suggesting that conflict processing commonly recruits the LIFG irrespective of the domain in which the conflict was encountered.

Despite such co-localization, the degree of LIFG activity that was recruited across tasks did not correlate substantially after correcting for multiple comparisons. Prior behavioral and neuroimaging studies that have failed to find correlated variation in conflict resolution performance have argued for domain-specific cognitive control that is delineated by syntactic (or perhaps verbal) boundaries. But such an account is difficult to reconcile with the co-localization findings reported here and elsewhere (e.g., January et al., 2009; Ye & Zhou, 2009), as well as with the breadth of behavioral evidence for shared conflict-control procedures (e.g., Hsu & Novick, 2016; Hussey et al., 2016; Novick et al., 2014; Nozari, Trueswell, & Thompson-Schill, 2016; Woodard et al., 2016). We therefore argued that an absence of such correlations does not inevitably repudiate domain-general arguments; instead, it might reflect idiosyncrasies in task properties and goals and the relative need for cognitive control that each of our tasks invokes because of differences in domain-specific representational quality and thus strength of the conflict signal that gives rise to LIFG activation.

Following Humphreys and Gennari (2014), our next prediction was that a cognitive-control "hub" in LIFG coordinates activity from disparate neural networks depending on information content and variation in conflict processing demands (see also van den Heuvel & Sporns, 2013). That is, each task's conflict contrast would reveal separate functional connectivity patterns with LIFG (see Section 5.3). Using PPI analyses, this prediction too was supported, resulting in a couple of noteworthy findings. First, our LIFG seed overlapped with that used by Humphreys and Gennari (2014), so the neural hub they observed for competitive interactions during sentence production and comprehension at least moderately corresponds to the one we find here. Moreover, their work indicated integration from both domain-general and domain-specific procedures during language processing; we extended these findings to show that such functional interconnectivity is modulated across syntactic and non-syntactic domains by a similar cognitive control hub. Second, this pattern is revealing alongside our co-localization findings and non-significant correlations. Insofar as there is a domain-general cognitive control system that resolves conflict during syntactic and non-syntactic tasks, there is inevitably a range in the amount of control recruited due to variation in the conflict signal that domain-specific representations generate in each individual task, which results in diverse connectivity patterns.

We detail each of these findings in what follows and discuss their implications.

5.2. A domain-general neural hub for resolving conflict

We used the most active LIFG voxels (within subregions pars opercularis and pars triangularis) during the Stroop task as each subject's individually identified ROI. Co-localization analyses utilizing this approach revealed consistent activation of LIFG when contrasting conflict with no-conflict conditions across the three other tested tasks. In addition to replicating earlier work showing co-localization of Stroop-conflict and syntactic ambiguity (January et al., 2009; Ye & Zhou, 2009), these results also parallel separate neuroimaging results showing LIFG recruitment for resolving conflict in item recognition and working memory updating tasks (Gray et al., 2003; Jonides & Nee, 2006). Importantly, our results were not dependent on the Stroop task as the localizer: similar co-localization results were also obtained when using conflict effects from any of the other tasks to create the seed ROI, and despite correction for multiple comparisons. Thus, our results extend previous findings across studies (and across subjects) by revealing a common neuroanatomical locus for conflict-control within subjects and within a single study. Further, by utilizing a single-subject approach that accounts for individual differences in brain anatomy as well as in task activation, these results demonstrate the importance of considering this variability when determining co-localization of shared cognitive control functions.

The universal recruitment of LIFG under high conflict demands in our study suggests a common functional-anatomical "hub" that engages when people must regulate behavior to resolve information-processing conflict in various contexts, including during syntactic processing. Posterior regions of LIFG may therefore broadly facilitate controlled cognition to avoid interruptions in focus, and a domain-general explanation of conflict resolution is appealing because we constantly encounter novel circumstances that jeopardize our attention

and maintenance of task goals in various ways. In other words, a multipurpose mechanism that enables us to cope with an array of conflict types is more efficient than having to rely on several distinct subsystems that must first detect the type of information content that is creating the conflict, before routing that evidence to the appropriate control mechanism.

One alternative interpretation of our findings is that the increased activation across tasks in LIFG reflects not conflict resolution specifically, but a range of cognitive challenges including sustained attention that also engage for complex tasks. Indeed, trials involving conflict took reliably longer for subjects to complete than trials without conflict, which is consistent with multiple interpretations. However, a broad "cognitive difficulty" interpretation is doubtful for two reasons. Firstly, our results did not change when we included RT as a within-task regressor of no interest, suggesting that any observed differences must be explained beyond time-on-task differences. Secondly, the multiple demand (MD) system is often framed as a constellation of regions that engage during cognitively demanding tasks (Duncan, 2010; Fedorenko, 2014). If our experimental manipulation reflected cognitive difficulty associated with a broader array of demanding cognitive processes, then we would expect the co-localization effect identified in LIFG to occur throughout more (if not all of) the MD system, as has been shown previously for hard vs. easy contrasts (Fedorenko et al., 2013). However, we found that MD regions did not universally engage during conflict resolution – in fact, *no MD regions aside from the LIFG* demonstrated consistent conflict effects across tasks, suggesting that our manipulation specifically tapped conflict-control procedures in a way that is distinct from cognitive difficulty per se. We interpret this selective LIFG result as a neural signature of conflict resolution, a mechanism that engages cognitive control to resolve competitive interactions. The lack of broader MD involvement renders a difficulty interpretation of our data unlikely.

5.3. Task-specific functional connectivity with a domain-general neural hub

We manipulated the presence or absence of conflict in each of the four tasks. However, the tasks differed in several important ways, including in stimuli characteristics and thus representation quality (e.g., single letters versus sentences), memory demands (e.g., recognition, storage, updating), and task goals (e.g., syntactic processing, recognizing items, color naming). The lack of correlation across tasks in the relative engagement of LIFG activity further suggested task diversity in cognitive control recruitment. We therefore tested the hypothesis that the LIFG hub would interact with separate neural systems, likely depending on these sources of variation. We used functional connectivity analyses (specifically, PPI analyses) to assess the extent to which the LIFG hub co-engaged with other brain systems during each task. The results of these analyses demonstrated that each task produced a distinct combination of brain regions that co-engaged with LIFG activity. We discuss these results by task.

Stroop—During Stroop-conflict, LIFG activation co-engaged with a region of left inferior temporal/fusiform gyrus commonly referred to as the visual word form area (VWFA), associated with word recognition and word meaning (Dehaene & Cohen, 2011). The use of single word stimuli in the Stroop task here may have differentially co-engaged the VWFA with the LIFG compared to the other tasks because those tasks used letters or sentences

presented as a whole. The exception, of note, was the memory updating task, which also included single word presentation, and this task also showed co-engagement between the LIFG and VWFA.

Given previous neuroimaging studies that have utilized Stroop, it may be surprising that the anterior cingulate cortex (ACC) did not co-activate with the LIFG, since the ACC is commonly recruited during conflict monitoring (Botvinick, Cohen, & Carter, 2004; Carter & van Veen, 2007). There might be a few reasons for this discrepancy. The ACC may be more engaged during incorrect compared to correct responses (Carter et al., 1998); but in our analysis, we modeled the entire trial duration and included both types of trials in order to boost statistical power, and this inclusion choice may have had some unintended consequences. First, although ACC activity often goes hand in hand with LIFG activity during both response- and representation-conflict, these effects may be separated in time, with ACC activity appearing during detection and other regions coming online later (e.g., Kerns et al., 2004). Second, and relatedly, modeling the entire trial duration may have sacrificed the detection of fine-grained temporal distinctions. Finally, conflict monitoring theories often link ACC activation with dorsolateral prefrontal cortical (DLPFC) activation rather than ventrolateral areas, and our lack of a significant ACC cluster coordinating with LIFG (which is within VLPFC) does not preclude a robust coordination between ACC and DLPFC regions.

Item recognition (Recent Probes)—When comparing RN to NRN trials, frontal and posterior regions co-engaged with LIFG, including right ACC, bilateral parahippocampal gyri, and left middle temporal gyrus. Previous neuroimaging studies using this item recognition task have reported other active brain regions in addition to LIFG, suggesting a specific network of regions that come online to manage the demands of this task (Jonides & Nee, 2006). Moreover, to our knowledge, only one other study examined functional connectivity between a LIFG seed region and other brain networks, identifying a somewhat different set of regions than the ones we find here (Nee et al., 2007). However, there is at least one important divergence between their functional connectivity analysis and ours: specifically, their seed region was identified on the basis of a behavioral and neural correlation, whereas ours was identified anatomically on a single-subject basis. This difference in seed region basis (i.e., anatomically- versus functionally-identified) might – at least in part – explain some of the discrepancies in the different regions identified here and in that study (Fedorenko et al., 2012).

One interesting finding from our functional connectivity analysis of the item recognition task is that of frontopolar cortex and bilateral parahippocampal gyrus activation, perhaps indicative of the increased memory demands required of this task compared to some of the other tasks utilized here. These regions have both been associated with episodic retrieval, and some have argued for a role of episodic retrieval during conflict resolution (Badre & Wagner, 2005; Bunge et al., 2004). Specifically, it has been proposed that conflict arises in this task because retrieval of a familiar recent-no trial activates the previous trial's context, which then interferes with the current trial's context. In this scenario, LIFG must cope with increased selection demands as frontopolar and temporal regions monitor and evaluate current contextual demands. Our findings may be consistent with this account; however we

are agnostic as to whether our analyses can distinguish between differing mechanisms of conflict resolution for this specific task, as they were not designed to do so.

Memory updating (n-back with lures)—Neural activity during lure trials as compared to target trials recruited a wide network of frontal and parietal regions that co-varied with posterior LIFG. Many of these regions overlapped with those reported by prior neuroimaging studies using the n-back task, including superior frontal regions, right motor cortex, bilateral supramarginal gyrus, and right dorsal posterior cingulate (Owen et al., 2005). Moreover, it is worth noting that both the memory updating task and the Stroop task involved single-word stimuli and, like the Stroop task, LIFG activity also co-engaged with VWFA during the memory updating task.

In addition to these regions, some clusters emerged that were fairly distinct from regions that are typically recruited during the n-back task, including occipital regions, the precuneus, cingulate and opercular cortex, and bilateral fusiform cortex. One possible explanation for this discrepancy involves the contrasts we used (i.e., lures > targets) that explicitly test for information-conflict. Typical neuroimaging results of the n-back task contrast a condition with memory demands against one without such demands (e.g., 2-back > 0-back) or against an unspecified baseline (e.g., lures > fixation). This difference may partly explain some differences in the resulting neural profile of LIFG coordination with other parts of the brain (but see Burgess, Gray, Conway, & Braver, 2011).

Another noteworthy finding within the memory updating task is the co-engagement between LIFG and regions of the cingulo-opercular network (CON), including anterior cingulate and central opercular cortex. It has been argued that CON recruitment occurs under conditions of uncertainty, or when performance needs to be monitored and adjusted over the course of a task (Dosenbach et al., 2006; Vaden et al., 2013). Moreover, the CON may implement these adjustments across trials (Dosenbach et al., 2007). Thus, it could certainly be the case that the memory and monitoring demands tapped by the updating task here were highest compared to the other tasks, thereby requiring coordination between LIFG and CON that was detected by our connectivity analyses.

Finally, the item recognition and memory updating tasks share memory demands that, one could reasonably argue, should result in co-engagement between the LIFG and the parahippocampal gyrus for both tasks. As discussed above, such a pattern was observed reliably for the item recognition task; however it appears conspicuously absent from the memory updating results. In fact, we did observe some LIFG-parahippocampal connectivity for the memory-updating task, yet the finding was just below threshold (thresholded t needed to exceed 3.09 to be significant; it was 2.89 for the memory updating task).

Syntactic ambiguity resolution—Activity in the LIFG during syntactic conflict (ambiguous vs. unambiguous contrast) coordinated with a constellation of other regions throughout the brain, including anterior prefrontal cortex, right middle frontal gyrus, left supplementary motor area, right precuneus, and bilateral cingulate cortex. This general profile replicates prior neuroimaging studies examining information-conflict during language processing. For instance, several of the regions emerged in two prior studies

examining syntactic conflict in language processing. Specifically, the right middle frontal gyrus and right precuneus emerged in a whole-brain analysis that contrasted strong versus weak syntactic conflict (January et al., 2009), and the left supplementary motor area demonstrated effects of syntax during sentence comprehension (Ye & Zhou, 2009).

To date, at least one previous study examined functional coupling of LIFG with other parts of the brain, finding that only left posterior medial temporal gyrus (pMTG) coordinated with LIFG during competition in sentence comprehension (Humphreys & Gennari, 2014). This coupling between LIFG and temporal regions sometimes occurs in studies of language comprehension (Gennari, MacDonald, Postle, & Seidenberg, 2007; Menenti, Gierhan, Segaert, & Hagoort, 2011; Whitney, Kirk, O'Sullivan, Lambon Ralph, & Jefferies, 2011). In our study, the coordination of LIFG and pMTG occurred but did not surpass our threshold; this pattern was true for other regions identified in the Humphreys and Gennari study, including the left precentral gyrus and left middle frontal gyrus. That experiment differs from ours in a few important ways however, including different stimuli, the manner in which the seed region was identified, and the contrast used to assess conflict effects. Some combination of these differences might explain the discrepancy between their functional connectivity findings and ours, which we leave to future work.

5.4. Summary of co-localization and network findings

Together, the results from the co-localization and functional connectivity analyses provide further evidence for a domain-general cognitive control hub in LIFG that interacts with distinct brain systems depending on task-specific conflict resolution demands. One practical appeal of such a coordinated system is that it allows for both domain-general and domain-specific conflict-control processing. LIFG might guide the resolution of conflict by sending and receiving information from the relevant domain-specific brain systems – depending on the content of that particular instance of conflict and how much control is required to resolve it. Note, however, that we only speculate that the networks tapped during conflict resolution may be domain-specific; we make no claims about the domain-specificity of the individual regions comprising those networks. Future work should test the directionality of this interaction between LIFG and other brain systems – that is, how LIFG receives information about conflict from these systems, or whether LIFG functions as conflict detector/resolver, signaling these systems to guide conflict resolution.

Though we have been arguing for a domain-general cognitive control system that contributes to conflict resolution across diverse tasks, including sentence comprehension, questions still remain about the boundary conditions that may constrain interpretations of how general the system is. For example, because our tasks all involved verbal material (using letter, word, or sentence stimuli), we did not test and therefore cannot rule out a verbal/non-verbal distinction in cognitive control. Previous work has successfully demonstrated such dissociations: e.g., performance on garden-path recovery correlates with verbal Stroop performance but not non-verbal Stroop performance (Vuong & Martin, 2014). This finding raises the possibility that there is some domain-specificity that mediates cognitive control during sentence comprehension, particularly alongside findings from neuropsychological studies that show patients with verbal cognitive control impairments but intact non-verbal

cognitive control ability (Hamilton & Martin, 2005). These are certainly important findings; however, as maintained throughout this paper, we caution against drawing strong conclusions about domain-specificity from non-significant correlations for theoretical reasons (see e.g., Miyake & Friedman, 2004). Other studies, moreover, do show clear correlations between sentence comprehension and non-verbal cognitive control (e.g., Nozari et al., 2016), so the findings on this issue are mixed. Here, we argue for domain-generality in LIFG that is unconstrained by *syntactic* boundaries, but future work should extend our approach to test how the combined co-localization and connectivity findings are modulated across verbal and non-verbal lines.

Prior studies have found distinct subregions of LIFG that functionally diverge according to syntactic and non-syntactic content, specifically when language regions are identified by comparing fairly short sentences to length-matched non-word lists (Fedorenko et al., 2012). Moreover, others have shown that brain networks engaged during story comprehension are separate from those comprising the MD system (Blank et al., 2014). Although these results suggest a sharp dissociation between language and other complex cognitive functions, as detailed in our introduction, those experiments were not designed to test for shared cognitive control procedures and thus may miss the possibility that some language processing tasks (e.g., those involving syntactic ambiguity and recovery from misinterpretation) nevertheless draw on general conflict-control mechanisms, as we have demonstrated here. That is, the materials for our language task were designed to compare syntactically ambiguous to syntactically unambiguous sentences, to identify whether syntactic conflict engages a brain region that is involved in handling conflict in non-syntactic tasks, not whether simple sentence processing (absent conflict) draws on the MD system or the LIFG. While there may be some functional-anatomical specificity for language (and more specifically, syntactic) processing, some linguistic tasks also theoretically require domain-general input from the neurobiological "hub" that handles information-processing conflict (for reviews, see Novick, Trueswell, & Thompson-Schill, 2010; Novick et al., 2005; Nozari & Thompson-Schill, 2015; see also January et al., 2009; Novick et al., 2009, 2014; Nozari, Mirman, & Thompson-Schill, 2016; Ye & Zhou, 2009).

5.5. Concluding remarks

In sum, these results are the first to demonstrate both task-independent co-localization of LIFG and task-dependent patterns of connectivity with this hub during conflict resolution, suggesting cooperation between domain-general and domain-specific systems during syntactic and non-syntactic processing. The findings suggest a neurobiological mechanism by which brain systems couple together to enable efficient focusing of human attention when dealing with mental conflict during language processing, item recognition, memory updating, and other complex cognitive tasks.

Acknowledgments

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.bandl.2016.12.006.
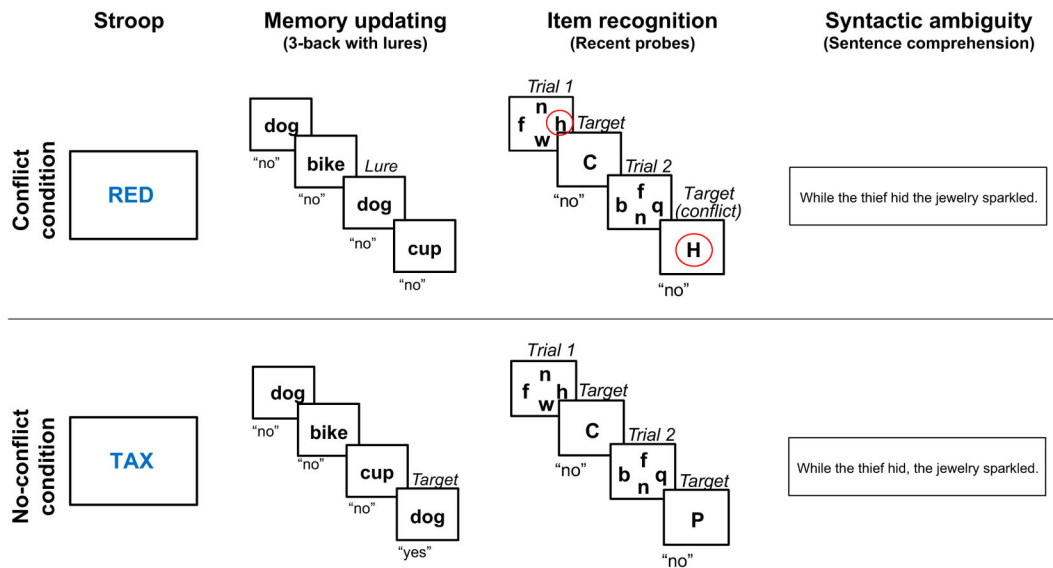
Fig. 1.
Example Conflict and No-Conflict (control) conditions in the four tasks. Trials with conflict (top row) are contrasted with no-conflict trials (bottom row). Note: the sentence comprehension example is truncated due to space constraints (see text for full example).
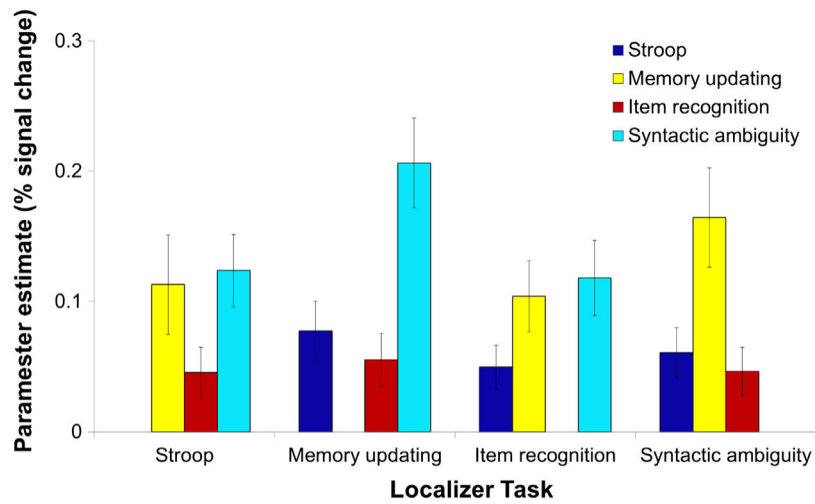
Fig. 2.
Conflict resolution commonly engages posterior LIFG across tasks. Single-subject co-localization analyses revealed cross-task LIFG activation using any of the four tasks as a functional "localizer" within anatomical ROIs (n = 25). Error bars indicate SEM. All comparisons are $p < 0.05$.
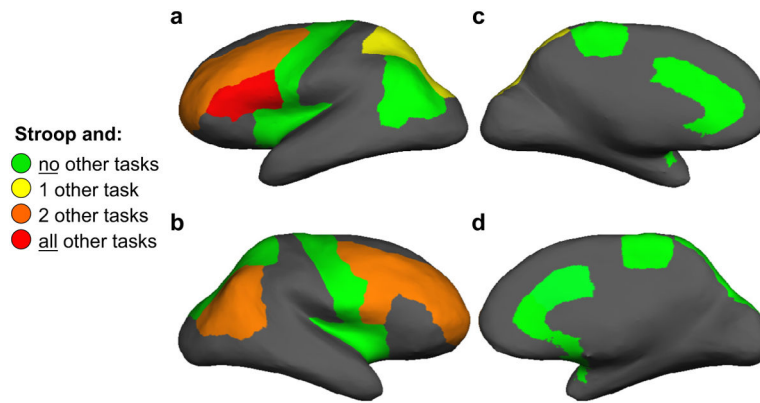
Fig. 3.

The number of tasks that demonstrated a significant conflict effect within each region of the Multiple Demand (MD) system. Lateral (a, b) and medial (c, d) views of MD regions. These anatomical ROIs do not show activation; rather, the color-coding represents how many tasks in addition to the Stroop localizer showed a significant conflict effect in ROIs that comprise the global MD system. As can be seen, co-localization analyses revealed that only the LIFG (in red) showed consistent activation across all four tasks. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
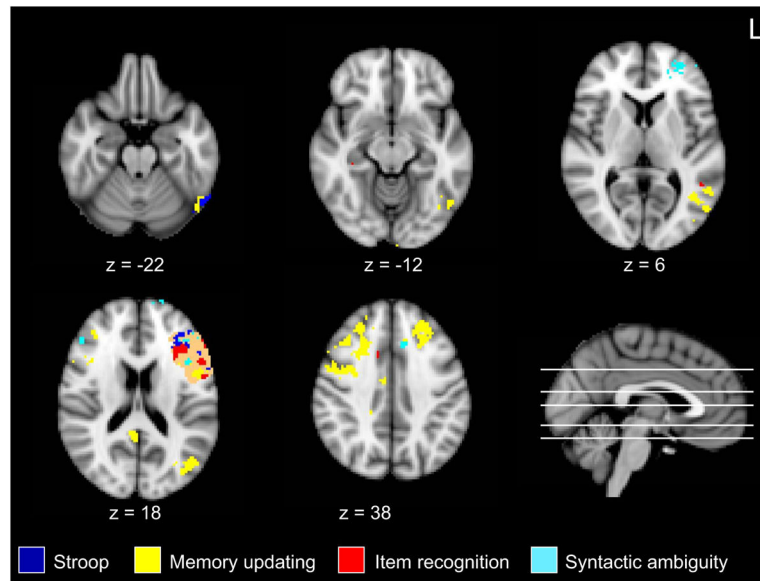
Fig. 4.
LIFG co-engages distinct, task-specific networks. We examined whole-brain networks within which activity co-varied with LIFG activation during each task's conflict contrast. Anatomical LIFG is shown in peach. The top five clusters from each task are shown here; for the full list, see Table S2.

Table 1

Activity in LIFG associated with conflict does not correlate across tasks. When correlating LIFG activation across tasks when each task is used as a localizer (designated in italics), we found no significant correlations in the degree of LIFG recruitment between tasks. Pearson correlation values (*r*) are reported in this table accounting for 25 degrees of freedom (# = *p* < 0.007).

	Stroop	*Memory updating*	Item recognition	Syntactic ambiguity
Stroop	1	.14	-0.23	-0.06
Memory updating		1	-0.01	.51 #
Item recognition			1	-0.09
Syntactic ambiguity				1

	Stroop	Memory updating	Item recognition	Syntactic ambiguity
Stroop	1	.45	-0.02	.10
Memory updating		1	-0.28	.25
Item recognition			1	-0.39
Syntactic ambiguity				1

	Stroop	Memory updating	*Item recognition*	Syntactic ambiguity
Stroop	1	-0.03	.02	-0.19
Memory updating		1	.25	.10
Item recognition			1	.06
Syntactic ambiguity				1

	Stroop	Memory updating	*Item recognition*	Syntactic ambiguity
Stroop	1	.28	-0.22	.08
Memory updating		1	-0.09	.08
Item recognition			1	-0.07
Syntactic ambiguity				1