



Review article

Conflict detection and resolution rely on a combination of common and distinct cognitive control networks



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ABSTRACT

Cognitive control can be activated by stimulus–stimulus (S-S) and stimulus-response (S-R) conflicts. However, whether cognitive control is domain-general or domain-specific remains unclear. To deepen the understanding of the functional organization of cognitive control networks, we conducted activation likelihood estimation (ALE) from 111 neuroimaging studies to examine brain activation in conflict-related tasks. We observed that fronto-parietal and cingulo-opercular networks were commonly engaged by S-S and S-R conflicts, showing a domain-general pattern. In addition, S-S conflicts specifically activated distinct brain regions to a greater degree. These regions were implicated in the processing of the semantic-relevant attribute, including the inferior frontal cortex (IFC), superior parietal cortex (SPC), superior occipital cortex (SOC), and right anterior cingulate cortex (ACC). By contrast, S-R conflicts specifically activated the left thalamus, middle frontal cortex (MFC), and right SPC, which were associated with detecting response conflict and orienting spatial attention. These findings suggest that conflict detection and resolution involve a combination of domain-general and domain-specific cognitive control mechanisms.

1. Introduction

Cognitive control is the ability to orchestrate thought and action in accordance with internal goals (Miller and Cohen, 2001). It has been conceptualized as a set of control functions that may include working memory, response selection, response inhibition, and task switching (Lenartowicz et al., 2010; Sabb et al., 2008). Its core system, the fronto-parietal network (FPN), meaningfully contributes to a variety of task contexts. The FPN allows rapid reconfiguration of information flow across multiple task-relevant brain networks, such as the visual network, auditory network, and default mode network (Cole et al., 2013). Alterations of this control system might contribute to a striking range of mental diseases (Cole et al., 2014). In the laboratory, various stimulus-response compatibility (SRC) tasks, such as the Stroop task (Stroop, 1935), the Eriksen flanker task (Gratton et al., 1992), and the Simon task (Simon and Small, 1969), have been employed to study cognitive control functionality. The SRC effect is the phenomenon in which performance is worse (i.e., slower and more erroneous) when mappings of stimuli to responses are incongruent than when they are congruent (Fitts and Seeger, 1953; Proctor and Vu, 2006).

Based on the distinct SRC tasks, several researchers have put

forward brain network models of cognitive control from an attention perspective. Fan et al. (2005) proposed three separable anatomical networks related to the components of attention. The alerting network, the orienting network, and the executive control network activate the thalamic, parietal, and anterior cingulate cortex, respectively. Corbetta and Shulman (2002) identified two partially segregated attentional systems. The top-down system, which includes parts of the intraparietal cortex and superior frontal cortex, is involved in preparing and applying goal-directed selection. The bottom-up system, which includes the temporoparietal cortex and inferior frontal cortex, is specialized for the detection of behaviorally relevant, salient or unexpected stimuli.

Different from two attention networks involved in cognitive control, Botvinick et al. (2001) proposed the conflict-monitoring (CM) model of cognitive control. This model describes a single, “all-purpose” conflict-control loop that can be recruited to generally handle different types of conflicting representations; the loop comprises the anterior cingulate cortex (ACC) for conflict detection and the prefrontal cortex for executive control (Botvinick et al., 2001). According to the CM model, many types of conflicts will yield highly similar patterns of brain activation because they share a centralized module of cognitive control. The expanded parallel distributed processing (PDP) model further

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suggests that the mechanisms of cognitive control are adaptive and self-regulating (Botvinick and Cohen, 2014). The model proposes that the anterior cingulate cortex implements the conflict monitoring by modulating the activity of control representations, and dopamine assists the adaptive gating by regulating the updating of control representations in the prefrontal cortex. However, according to the dimensional overlap (DO) model proposed by Kornblum et al., SRC effects can occur independently when at least two of three dimensions (task-relevant stimulus dimension, task-irrelevant stimulus dimension, and response dimension) overlap (Kornblum, 1994). In a typical Stroop task, the SRC effect involves stimulus-based processing (S-S conflict) as the conflict stems from incongruence between task-relevant (S_R , e.g., ink color) and task-irrelevant (S_I , e.g., word meaning) stimulus features (Egner et al., 2007; Liu et al., 2010). In a typical Simon task, the SRC effect involves response-based processing (S-R conflict) as the conflict results from incongruence between a task-irrelevant stimulus feature (S_I , e.g., the location of the stimuli) and a response feature (R , e.g., button press) (Egner et al., 2007). Under this definition, S-S and S-R conflicts belong to distinct DO types and are resolved by distinct control mechanisms. Supporting the DO model, the domain-specific model further proposes that specific conflict-control loops are involved in processing S-S and S-R conflicts (Egner, 2008). The model suggests that the SRC effects that stem from S-S and S-R conflicts uniquely activate specific brain regions because distinct cognitive control mechanisms are engaged in parallel by S-S and S-R conflicts.

Functional magnetic resonance imaging (fMRI) studies might provide insight into these theoretical debates and issues because they have the potential to demonstrate whether S-S and S-R conflict processing engage common or distinct brain mechanisms. Previous fMRI studies manipulating S-S and S-R conflicts have found that the brain uses distinct but parallel cognitive control mechanisms to resolve these different forms of cognitive interference (Egner et al., 2007; Liston et al., 2006; van Veen and Carter, 2005). In contrast, some studies have found that although the specific brain activation patterns are not identical across conflict domains, S-S and S-R conflicts share a common neural mechanism of attentional control and top-down modulation (Fan et al., 2003; Jiang and Egner, 2014; Kim et al., 2010; Kim et al., 2011; Liu et al., 2004; Milham et al., 2001). Some studies have even found completely overlapping activations across conflict domains (Peterson et al., 2002).

The differing results in conjunction with confounding factors make it difficult to obtain a clear understanding of the conflict-control processes in the human brain. First, the heterogeneity of the results is partly due to diverse experimental paradigms developed by various research groups that have aimed to address different aspects of cognitive control, such as motivation (Soutschek et al., 2014), attentional switching (Kim et al., 2012), and anticipatory control processes (Aarts et al., 2008). Second, it is unknown whether activation patterns reflect information processing relevant to the cognitive control process itself or serve incidental functions. Although an fMRI study harnessed multivoxel pattern analysis (MVPA) decoding S-S and S-R conflicts to overcome these limitations of traditional studies and showed a hybrid architecture of conflict processing entailing both domain-specific and domain-general components (Jiang and Egner, 2014), a single study is unlikely to provide decisive results regarding cognitive control processing.

Therefore, it is crucial to pool prior studies together and examine the core common and distinct conflict-processing networks in the human brain by combining theory-driven and data-driven approaches. One method of meta-analysis, activation likelihood estimation (ALE) (Turkeltaub et al., 2002), allows statistically verifiable concurrence across functional neuroimaging studies, revealing regions with the highest “likelihood” of activation, i.e., regions in which concurrence is highest.

The main goal of the current study is to assess whether cognitive control mechanisms underlying DO conflicts are general or distinct by

performing a meta-analysis of the results of 111 recent neuroimaging studies. Three different patterns of results that relate to different cognitive control models are possible. 1) Domain-general activation. According to the CM model and expanded PDP model, which initially insisted on an all-purpose control module, cognitive control areas associated with S-S and S-R conflict processing would be activated completely consistently. 2) Domain-specific activation. Based on the DO model and the domain-specific model, S-S and S-R conflicts would show separate neural activation patterns because of their conflict-specific processing strategies. 3) Mixed activation. However, considering the inefficiency of conflict processing by a unitary control process and the impossibility of endless control mechanisms for each potential source of conflict, the combination of domain-general and domain-specific models is a more reasonable explanation. Specifically, we expected a hybrid neural architecture of conflict-control involving both specific and general brain areas to process S-S and S-R conflicts.

2. Methods

2.1. Literature search and organization

2.1.1. Study identification

Four independent researchers conducted a thorough search of the literature for fMRI studies examining S-S and S-R conflict processing in humans. The terms used to search the online citation indexing service PUBMED (through July 2017) were “fMRI” and “Stroop/Flanker/SNARC/Simon/Navon/Global-Local” by the first researcher, and “functional magnetic/resonance imaging/fMRI” in the abstract and “Stroop/Flanker/SNARC/Simon” in all fields by the second researcher. The terms used to search the online citation indexing services PUBMED (through July 2017), EBSCO, and Web of Science were “fMRI/brain” and “Stroop/Flanker/SNARC/Simon/conflict/Navon/Global-Local” by the third researcher. The terms used to search the online citation indexing service PUBMED (through July 2017) and Google Scholar were “fMRI/MRI/PET”, “Stroop/Flanker/SNARC/Simon/Navon/stimulus-response compatibility” and “response eligible” by the fourth researcher. All resulting articles were pooled into a database, and redundant entries were eliminated. The initial search results were merged to produce a total of 1832 articles. Several exclusion criteria were then applied to eliminate articles that were not directly relevant to the current study. The exclusion criteria were as follows: 1) the study was not a primary empirical study (e.g., review articles); 2) the study did not report results in standard stereotactic coordinate space (either Talairach or Montreal Neurological Institute, MNI); 3) the study used tasks unrelated to the DO framework, for example, the stop-signal task (Hendrick et al., 2010), which has been widely used to study inhibition control, but involves no overlap among stimulus or response dimensions; 4) the study was related to S-S or S-R conflict processing that was not “pure” due to the overlapping of the relevant stimulus dimension, irrelevant stimulus dimension, or response dimension with each other; for example, the Flanker task mixed with visual search (Wei et al., 2013) was not “pure” conflict, nor was the study influenced by cuing (e.g., Forstmann et al., 2008a) or affective factors (e.g., Comte et al., 2016); 5) the study was of structural brain analyses (e.g., voxel-based morphometry or diffusion tensor imaging); 6) the study was solely based on region of interest (ROI) analysis (e.g., using anatomical masks or coordinates from other studies); 7) the study was of a distinctive population of individuals whose brain function may deviate from those of normal, healthy adults (e.g., children, aging adults, or substance-dependent individuals); and 8) the study did not report the coordinates for the healthy adult group alone. Variability was accepted among methods in which subjects were instructed to report decisions during the tasks (i.e., verbal, nonverbal button press). This search process resulted in 111 articles in the final database (listed in Supplementary Table 1). See Fig. 1 for details regarding the literature search process.

During data extraction, studies were grouped by the following

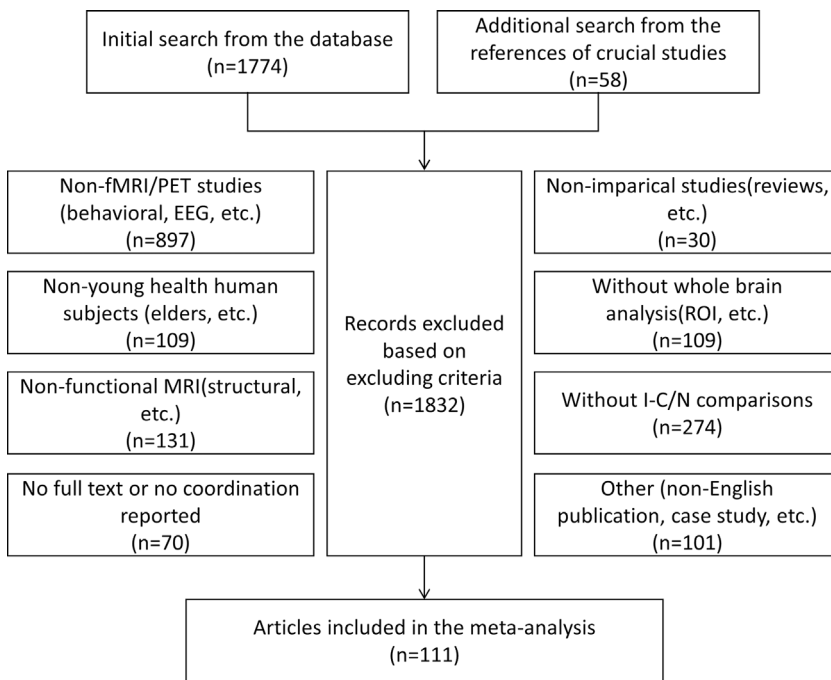


Fig. 1. Flow diagram for the literature search.

spatial normalization schemes according to coordinate transformations implemented in the GingerALE toolbox (<http://brainmap.org>, Research Imaging Center of the University of Texas Health Science Center, San Antonio, Texas): using FSL (<http://www.fmrib.ox.ac.uk/fsl>) to report MNI coordinates, using SPM (<http://www.fil.ion.ucl.ac.uk/spm>) to report MNI coordinates, using other programs to report MNI coordinates, using Brett methods to convert MNI coordinates into Talairach space (Brett et al., 2001) and using a Talairach native template. Lists of coordinates that were in Talairach space were converted into the MNI space using their original normalization schemes. For the Brett-Talairach list, coordinates were converted back into the MNI space using reverse transformation following Brett et al. (2002) (i.e., tal2mni). For the native Talairach list, BrainMap's Talairach-MNI transformation was used (i.e., tal2icbm other). A master list of all studies was created by combining all the coordinates in the MNI space in preparation for the ALE meta-analyses in GingerALE.

2.1.2. Experiment categorization

To test hypotheses regarding the common and distinct brain networks for processing S-S and S-R conflicts, coordinates based on three types of conflicts were categorized: S-S conflicts, S-R conflicts, and S-S & S-R conflicts. The term “experiments” was adopted, as used by the BrainMap database, to refer to individual regressors or contrasts typically reported in fMRI studies. Any conflicts due to overlap between task-relevant or task-irrelevant stimuli with response were considered S-R conflicts. This modulation included type 2 (conflict between task-relevant stimulus and response dimension, e.g., response with left hand to the right arrow (Sylvester et al., 2003)), type 3 (conflict between task-irrelevant stimulus and response dimension, e.g., Simon task (Forstmann et al., 2008b)) and type 5 (conflict combining type 2 and 3, e.g., Hedge and Marsh task (Li et al., 2015)). Any conflicts from overlap between task-relevant stimuli and task-irrelevant stimuli were regarded as S-S conflicts. Conflicts containing S-S and S-R conflicts simultaneously were regarded as S-S & S-R conflicts. Considering that both contrasts (Incongruent (I) > Neutral (N) and Incongruent (I) > Congruent (C)) are widely used to infer the conflict effect, they were combined in this analysis (Krebs et al., 2013; Milham et al., 2002).

2.2. ALE

The algorithm adopted for ALE was first implemented by Turkeltaub et al. (2012). ALE models the activation foci as 3D Gaussian distributions centered at the reported coordinates and then calculates the maximum of each focus within an experiment, creating modeled activation maps. The convergence of activation patterns across experiments is calculated by taking the union of the above modeled activation maps. In contrast analysis, a null distribution that represents ALE scores generated by random spatial overlap across studies is estimated through a permutation procedure. The studies of S-S and S-R types were pooled and then randomly divided into two groups with the same number as the real groups. Then, a contrast of ALE scores for the random groups was computed. This procedure was repeated many times, forming the null distribution. The ALE map contrast computed from the real activation coordinates is then tested against the ALE scores from the null distribution, producing *p*- and *z*-maps. This procedure could remove the effect of different sample sizes across two contrasting conditions. For a detailed description, see Eickhoff et al. (2011).

Six different ALE analyses were conducted with GingerALE 2.3.6 (Turkeltaub et al., 2012): one for the main analysis of all conflicts from the set of included studies, two individual analyses of S-S and S-R conflicts sub-listed, two subtraction ALE analyses for the contrast between S-S and S-R conflicts, and one conjunction ALE analysis for the common brain activation of S-S and S-R conflicts. For single study, ALE maps were computed at a cluster-level family-wise-error (FWE) corrected threshold at $p < 0.01$ with a cluster-defining threshold of $p < 0.001$ (uncorrected) and 1000 permutations (Eickhoff et al., 2017; Eickhoff et al., 2012; Eickhoff et al., 2016). Since the minimum cluster threshold was calculated by the permutation result, the value for different single studies could be different. For the contrast analysis, because the alternatives of false discovery rate (FDR) correction have problems and are not recommended (Eickhoff et al., 2017), we adopted a conservative uncorrected threshold at $p < 0.01$ to avoid Type II errors, as the single study results had already been thresholded, and added a minimum cluster size criterion of 400 mm³ contiguous supra-threshold voxels.

2.2.1. Main analysis of all conflicts in all studies

All 111 studies were included for the S-S conflicts, S-R conflicts, and

S-S & S-R conflicts in the main analysis, which consisted of 1663 foci from 141 experiments (contrasts).

2.2.2. Individual analyses of S-S and S-R conflicts in the sub-lists

Two ALE analyses were conducted based on the sub-lists that categorized different experiments into S-S and S-R conflicts. For the S-S conflict analysis, 917 foci from 75 experiments were included. The S-R conflict analysis consisted of 294 foci from 27 experiments.

2.2.3. Subtraction and conjunction analyses

We contrasted brain areas that were selectively or preferentially activated by S-S conflicts versus S-R conflicts and evaluated the overlapping brain activations of the two types of conflicts by examining the conjunction results. A permutation test of randomly distributed foci with 10,000 simulations was run to determine the statistical significance of the ALE maps (Eickhoff et al., 2011; Fox et al., 2013).

3. Results

The all-inclusive analysis of 141 experiments showed significant activation of a large cluster, including the left supplementary motor area (SMA), right ACC, bilateral inferior frontal cortex/dorso lateral prefrontal cortex (IFC/DLPFC), bilateral inferior parietal cortex (IPC), bilateral superior parietal cortex (SPC), bilateral insula, bilateral thalamus, and right caudate (see Fig. 2 and Table 1).

S-S conflicts activated a subset of the aforementioned networks, including the bilateral IFC/DLPFC, right ACC from the adjacent left SMA, left IPC, right SPC, left inferior occipital cortex (IOC), and bilateral insula. S-R conflicts activated the left ACC, left SMA, bilateral insula, left thalamus, and right SPC (see Table 2).

Common activation of S-S and S-R conflicts occurred in the left SMA extending to the dorsal ACC, bilateral insula, and right SPC. Contrasting the activation caused by S-S versus S-R conflicts, we found that S-S conflicts significantly activated the following regions to a greater degree: the left IFC, left middle frontal cortex (MFC), left superior occipital cortex (SOC), left SPC, and right ACC. The left thalamus, right MFC, and right SPC showed greater activation with S-R conflicts than with S-S conflicts (Fig. 3 and Table 3).

4. Discussion

A fundamental challenge to goal-directed behavior is that

multitudes of stimuli compete for control over our actions. Conflict control, i.e., the ability to resolve this competition, is consistent with an organism's current goals. From a theory-driven perspective, we discovered common neural networks in S-S and S-R conflict processing, including the left SMA/dorsal ACC, bilateral insula, and right SPC. In addition, distinct neural substrates and specific functions subserved the processing of S-S and S-R conflicts. The regions involving the left IFC, left MFC, left SOC, left SPC, and right ACC that were activated significantly more by the S-S conflicts were those involved in biasing the processing toward semantic-relevant attributes and semantic conflict monitoring (Van Ettinger-Veenstra et al., 2012; Coderre and van Heuven, 2013). In contrast, the left thalamus, right MFC, and right SPC were activated significantly more by the S-R conflicts, which are sensitive to the response conflict (van Veen and Carter, 2005), response inhibition (Ray Li et al., 2008), and spatial attention (Coull and Frith, 1998; Chen et al., 2006; Dharmadhikari et al., 2015). Similarly, a classifier analysis of data from the BrainMap database revealed certain subcomponents of cognitive control that might be uniquely classified, whereas others could not be, suggesting that these different components may vary in their ontological reality (Lenartowicz et al., 2010). Overall, these findings support an existing proposal that a hybrid neural architecture of conflict control involves both global (domain-general) and modular (domain-specific) components (Jiang and Egner, 2014).

4.1. Core brain networks of S-S and S-R conflicts

The current study has identified a fronto-parietal and cingulo-opercular network that resolves both S-S and S-R conflicts and possibly other conflicts. The four areas of the network play a pivotal role in supervisory attentional control, as revealed by minimum conjunction analysis. The current results are consistent with those of previous studies reporting common activations (Cieslik et al., 2010; Dosenbach et al., 2006; Fan et al., 2003; Wager et al., 2005) and in meta-analytic studies of interference resolution (Nee et al., 2007; Niendam et al., 2012). These studies suggest that the fronto-parietal and cingulo-opercular might form a core system that implements goal-directed task sets by a general top-down control mechanism in response to conflict (Cieslik et al., 2010; Dosenbach et al., 2006; Wager et al., 2005). Activation of these regions was correlated with performance on conflict-processing tasks, implying broad functions in monitoring and implementing control during conflict processing (Fan et al., 2003; Miyake et al., 2000; Wager et al., 2005). Some researchers propose that the

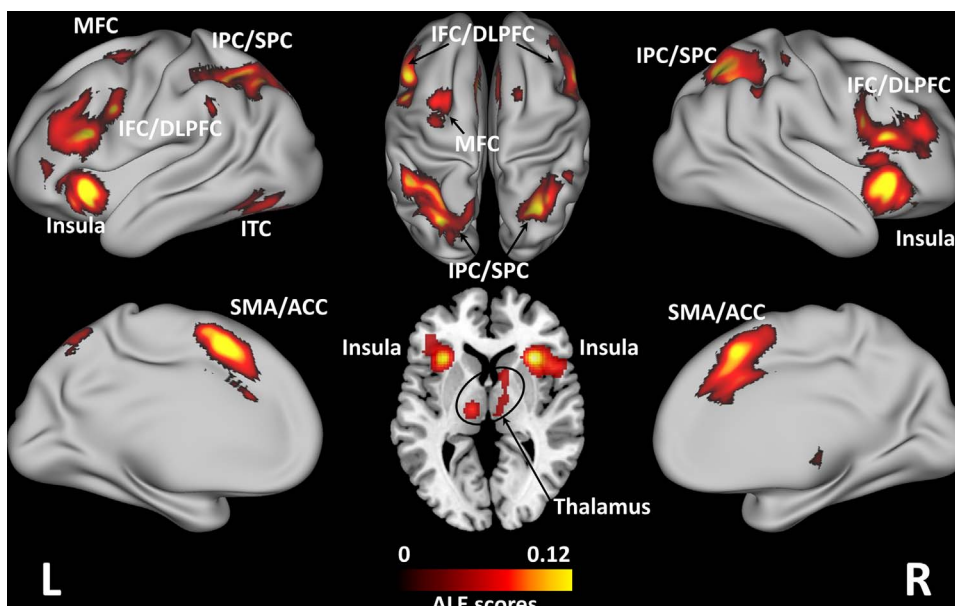


Fig. 2. Overview of significant clusters (cFWE, $p < 0.01$) in the ALE meta-analysis across all conflict sets in 141 experiments. The analysis demonstrated the primary brain regions with significant activation.

Table 1Brain areas commonly activated by all studies from the ALE analysis (cFWE, $p = 0.01$ and uncorrected cluster-defining $p = 0.001$).

Region	BA	L/R	x	y	z	ALE ($\times 10^{-2}$)	Volume (mm^3)
Supplementary Motor Area	6	L	-2	16	50	11.14	17,272
Anterior Cingulate Cortex	32	R	6	24	36	6.37	
Superior Frontal Cortex	6	R	18	4	64	2.59	
Inferior Parietal Cortex	40	L	-42	-42	46	7.32	15,632
Precuneus	7	L	-28	-68	36	7.20	
Insula		R	34	22	2	11.25	11,176
Inferior Frontal Cortex	9	L	-46	10	30	10.83	9448
Inferior Frontal Cortex	9	R	48	14	26	9.02	9168
Superior Parietal Cortex	7	R	32	-54	48	8.10	8176
Inferior Parietal Cortex	40	R	48	-38	48	3.84	
Insula		L	-32	22	0	10.76	6992
Inferior Frontal Cortex	46	L	-44	36	2	3.29	
Inferior Occipital Cortex	37	L	-48	-62	-12	4.38	4376
Thalamus		R	14	-6	12	4.20	3368
Caudate		R	12	8	2	3.42	
Middle Frontal Cortex	6	L	-26	-2	54	5.60	3008
Thalamus		L	-12	-16	4	4.92	2016

fronto-parietal and cingulo-opercular networks (multiple-demand cortex, MDC), as domain-general networks are likely to support diverse cognitive processes (Hampshire and Sharp, 2015). In addition, lesion studies have provided evidence that patients with ACC, prefrontal cortex, or insula lesions have deficits in conflict-related behavioral modulation (di Pellegrino et al., 2007), conflict control (Mansouri et al., 2009), or inhibition of motor responses (Bonnelle et al., 2012). MRI studies have further investigated the neural correlates of conflict detection and resolution in early childhood and found developmental changes in thickness and activation of the medial PFC and ACC. Consistent with the current study, a number of previous studies have noted that subcortical regions inhibit inappropriate responses (Kelly et al., 2004; Wager et al., 2005). Thus, a neural implementation of executive function, such as inhibition, is likely to involve a distributed network including both cortical and subcortical areas.

Although the signature of conflict-control stemming from the difference between incongruent and congruent and/or neutral trials (Krebs and Egner, 2013), it is noteworthy that inconsistent neural activation patterns in conflict studies might have resulted from the different use of congruent or neutral trials as contrast for incongruent trials. To partly explain the contribution of different baselines to inconsistent neural activation patterns in conflict fMRI studies, we systematically tested the differences between “incongruent-neutral” and

“incongruent-congruent” in all-inclusive conflicts (see Supplementary Tables 2 and 3). We found that the conflict-processing networks using congruent and neutral trials as baselines are similar. However, compared with congruent trials, neutral trials in contrast to incongruent trials indicated greater activation in the dorsal ACC and medial frontal gyrus that related with the competition between the relevant and irrelevant dimensions (Milham et al., 2002), interference monitoring and suppression (Blasi et al., 2006). By contrast, compared with neutral trials, congruent trials as contrast for incongruent trials indicated greater activation in the DLPFC and PC, reflecting the increased attentional requirements (Posner and DiGirolamo, 1998) and the facilitation effects (Mitchell, 2005; Cohen Kadosh et al., 2008; Carter et al., 1995).

4.2. Distinct brain networks associated with S-S and S-R conflicts

In this study, we found specific conflict-control loops for the S-S and S-R conflicts, which supports the notion that conflict-driven control mechanisms operate in a conflict-specific manner (Egner, 2008; Egner et al., 2007; Wendt et al., 2006).

The specific brain areas involved in S-S conflict processing in the current meta-analysis were mostly located in the left hemisphere, supporting previous findings of hemisphere dominance. In a review of

Table 2Brain areas activated by S-S or S-R conflicts from the ALE analysis (cFWE, $p = 0.01$ and uncorrected cluster-defining $p = 0.001$).

Region	BA	L/R	x	y	z	ALE ($\times 10^{-2}$)	Volume (mm^3)
S-S							
Inferior Frontal Cortex	9	R	46	12	26	5.83	14,192
Insula		R	34	22	4	5.70	
Middle Frontal Cortex	9	R	46	32	24	3.72	
Inferior Frontal Cortex	44	R	48	16	4	3.41	
Inferior Frontal Cortex	47	R	34	28	-12	2.21	
Supplementary Motor Area	6	L	0	16	50	6.19	12,976
Anterior Cingulate Cortex	32	R	8	22	38	4.92	
Inferior Parietal Cortex	7	L	-32	-54	52	5.81	10,040
Inferior Frontal Cortex	9	L	-46	10	30	9.41	9040
Insula		L	-32	22	-2	6.40	4752
Superior Parietal Cortex	7	R	32	-56	50	4.16	2688
Inferior Occipital Cortex	37	L	-48	-62	-14	2.98	2472
S-R							
Anterior Cingulate Cortex	24	L	-6	12	48	4.11	4168
Supplementary Motor Area	6	L	2	4	58	1.75	
Superior Parietal Cortex	7	R	28	-56	50	2.12	2352
Insula		R	32	20	4	3.52	1984
Insula		L	-32	20	4	2.42	1552
Thalamus		L	-16	-18	16	2.22	1376

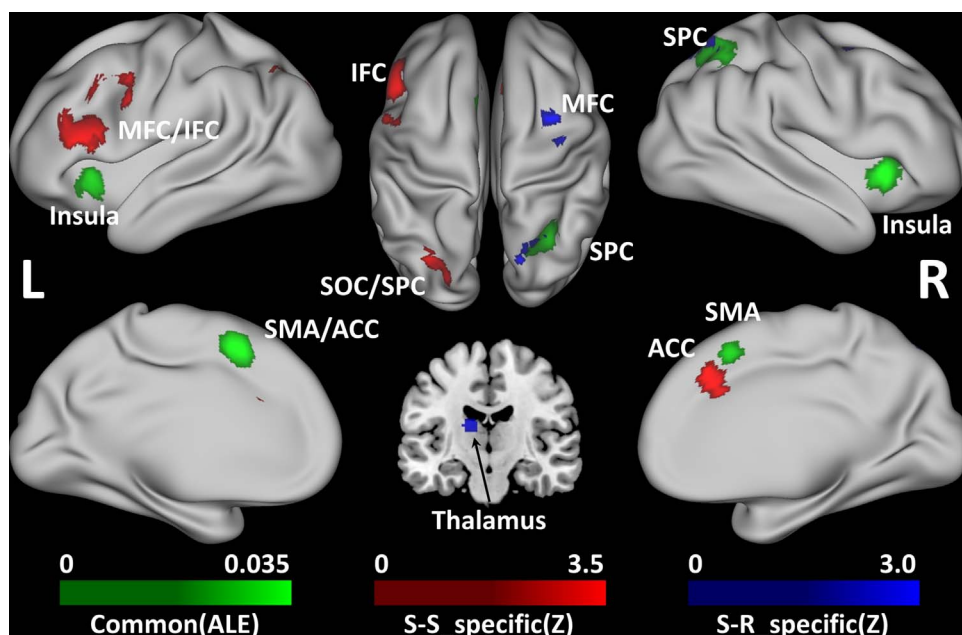


Fig. 3. Overview of significant clusters (uncorrected, $p < 0.01$) in the ALE meta-analysis showing patterns of common and specific activation across S-S and S-R conflicts. The analysis demonstrated the primary brain regions with significant activation. Common and specific activations of distinct conflicts are indicated with different colors. The green bar represents the ALE values of common activation, and the red and blue bars represent the Z values of specific activation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the S-S conflict-relevant literature, MacLeod (1991) suggests that S-S conflicts have greater interference effects in the left hemisphere than in the right hemisphere because of the dominant role of the left hemisphere in speech processes and the processing of verbal distractions. The left-hemisphere BA 44 is part of Broca’s area, a region involved in language function and the processing of semantic information (Wagner et al., 1998). Furthermore, the left IFC is associated with increased cognitive load and improved attention (Schaefer et al., 2015), as well as the suppression of response tendencies (Forstmann et al., 2008b). In semantically related conflict tasks, the left IFC is thought to implement cognitive control via suppression of irrelevant semantic information (Coderre and van Heuven, 2013). Some studies suggest that the left PC but not the right PC is relevant to attentional shifting between task-relevant stimuli (Dodds et al., 2011) and mediates the allocation of attentional resources toward the task-relevant stream such that the processing of the information is up-regulated (Liu et al., 2004). The right ACC is frequently engaged across a wide distribution of language-related cognitive tasks (Van Ettinger-Veenstra et al., 2012), speech initiation (Chang et al., 2007), and selective attention tasks (Lévesque et al., 2006). In addition, the possibility of increased top-down modulation comes from the left PFC and the left PC to the visual processing

center, the left OC (Gazzaley et al., 2007). The activities in these areas suggest that a resource reallocation strategy might be used to emphasize the processing of the S-S conflicts, both at the stimulus input and the response levels of conflict control. However, the lateralization in the S-S conflicts might be attributed to the factors of response hand or stimulus presentation. To exclude these confounding factors, we computed the specific activations in the response hand and stimulus presentation. No lateralization was found (see Supplementary Tables 2, 4, and 5). Therefore, the dominant left hemisphere in processing the S-S conflicts might reflect the conflict processing related with speech and language.

The S-R conflict processing was distinguished by modulating activity in the left thalamus, right MFC, and right SPC. In S-R conflict tasks, the incongruent condition requires inhibition of the automatic tendency to react to the bottom-up-driven processes of the target stimulus, a top-down-modulated reorienting toward the opposite side, and an initiation of response by the contralateral hand. Some fMRI studies have indicated that these processes are associated with increased activity in the thalamus, which plays important roles in response conflict (van Veen and Carter, 2005), mediating motor response inhibition (Ray Li et al., 2008), and attentional orienting (Dharmadhikari et al., 2015).

Table 3
Brain areas commonly and specifically activated by S-S and S-R conflicts from the ALE analysis (uncorrected $p = 0.01$ and a minimum cluster size of 400 mm^3).

Region	BA	L/R	x	y	z	ALE ($\times 10^{-2}$)	Volume (mm^3)
Common							
Supplementary Motor Area	32	L	-6	14	48	4.08	3424
Supplementary Motor Area	6	L	0	4	56	1.48	
Insula		R	32	20	4	3.52	1816
Insula		L	-32	20	4	2.42	1352
Superior Parietal Cortex	7	R	28	-56	50	2.12	960
S-S specific							
Middle Frontal Cortex	6	L	-45	6	38	371.90	4536
Inferior Frontal Cortex	44	L	-48	16	20	354.00	
Middle Frontal Cortex	46	L	-49	18	22	343.16	
Superior Occipital Cortex	31	L	-26	-76	34	371.90	1808
Superior Parietal Cortex	7	L	-26	-68	34	335.28	
Anterior Cingulate Cortex	32	R	4	26	34	354.01	1384
S-R specific							
Thalamus		L	-14	-15	15	389.06	760
Superior Parietal Cortex	7	R	20	-60	52	335.28	592
Middle Frontal Cortex	6	R	28	-4	54	371.90	592

Some fMRI studies have indicated that these processes are associated with increased activity in the MFC, which plays important roles in response inhibition, the reorientation response (Cieslik et al., 2010), and orientation of spatial attention (Chen et al., 2006). Different from an adjacent region of the right posterior parietal cortex, i.e., the intraparietal sulcus, which is associated with both spatial and non-spatial forms of attentional processing, the SPC is associated more exclusively with spatial attention (Coull and Frith, 1998).

Results from previous neuroimaging studies and the current study support the notion that the human brain flexibly adopts and independently controls conflict-specific processing strategies. We propose that these strategies involve biasing, such that stimulus representations are biased to resolve stimulus-based conflict, whereas motor programming and spatial attention are biased to resolve response-based conflict.

Importantly, domain-general versus domain-specific neural implementation of conflict-control processing was threshold-dependent (Jiang and Egner, 2014). The results of the meta-analysis indicated that a more lenient threshold produced greater common and specific activations, whereas a more stringent threshold led to less common and specific activations (see Supplementary Fig. 1 and Supplementary Table 6). These findings suggest that previous single imaging studies or meta-analyses were affected by the arbitrary nature of statistical thresholding. They also remind us that future fMRI research could use multivoxel pattern analysis (MVPA), which is not characterized by mean activation differences between conditions and could overcome the threshold-dependent limitation (Howard et al., 2009).

4.3. A schematic illustration of cognitive control processing

Based on the findings of common and distinct networks involved in processing S-S and S-R conflicts, we devised a schematic illustration to summarize the domain-general and domain-specific models of conflict-driven cognitive control (see Fig. 4). We grouped different brain regions based on their roles in different types of conflict processing; however, each region may serve multiple functions and interact with other brain areas in far more complex manners. One possible sketch for such a hybrid executive processing architecture might show that a central, domain-general resource is required for setting up and operating a task set, but the various sensory and motor pathways biased by this task set are processed by specific conflict mechanisms that rely largely on domain-specific, peripheral resources. For example, information regarding different conflicts, such as S-S conflicts involving the overlap of the task-relevant and task-irrelevant dimensions, would enter at the input level, whereas S-R conflicts involving the overlap of task-relevant/task-irrelevant dimension and response dimension would enter at the representation level. The processing of S-S conflicts was distinguished by the modulation of activity in the left IFC, left SPC, left SOC and right ACC. Most of these specific brain areas are located in the left hemisphere and are involved in verbal and semantic processing. The left SOC encodes the visual processing stream to the left SPC and is associated with increased shifted attention to relevant task information and the suppression of semantic information. The right ACC monitors semantic-

related conflict and sends the signal to an integrative system (i.e., the left IFC). By contrast, the S-R conflicts were distinguished by modulation of activity in the left and right SPC. These areas inhibited the automatic tendency to react toward the bottom-up-driven processes of the target stimulus, facilitated top-down-modulated reorienting toward the opposite side, and initiated the response by the contralateral hand. These specific regions, together with a general conflict-processing network (i.e., a crucial fronto-parietal and cingulo-opercular network) and possibly other regions, facilitate the processing of distinct conflicts.

4.4. Caveats

Two methodological caveats must be noted. First, we did not collect sufficient studies about pure S₁-R conflict. In addition to S₁-R conflict, we included S_R-R and S_R-R & S₁-R conflicts to obtain a broader S-R conflict group. Although the combined S-R conflict group is more representative and general, limited studies of these different types may produce less specific regions of S-R conflicts. Second, the coordinate-based ALE method calculates the likelihood of peaks based exclusively on coordinates, which may not reflect real likelihoods. Recently, it has been suggested that more information might be developed using a map-based analysis to calculate the activation likelihood (Maumet and Nichols, 2015). However, this undertaking was not possible in this study because the contrast and standard error maps are not widely shared.

The mechanisms of cognitive control in conflict processing have been studied and discussed for decades, but the results have generated more contradictions than consensus. This meta-analysis discovered certain key brain regions responsible for processing different conflicts, but the exact roles of these regions, how these regions interact with one another, and how they modulate information processing remain areas of intense investigation. Future studies must further address some of these issues. A possible way to obtain information regarding the flow of conflict processing is to examine the predictive efficiency from one region to another (Cole et al., 2016).

As for specificity, the notion of a cognitive module has been discussed (Egner, 2008; Liu et al., 2010). However, the modular idea attributing certain brain regions to specific functions leads to all-or-nothing conclusions, which may be a dead end. With increasing studies on functional connectivity and pattern analyses, it has been reported that the cognitive control network functions as a hub that could easily transfer from one state to the other (Cole et al., 2013). Therefore, it is probably more reasonable to regard the difference between different conflict types as a state difference rather than two different types of control mechanisms.

4.5. Conclusion

We investigated the relative contributions of conflict-specific and conflict-general control mechanisms in the human brain by employing a meta-analytic approach. We documented that S-S and S-R conflict-control processes can be effectively interpreted by a combination of

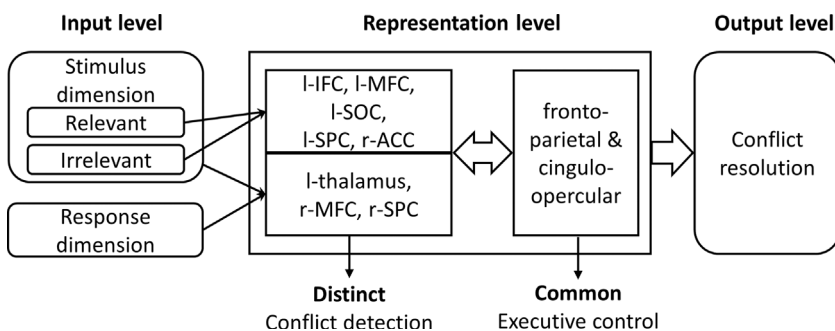


Fig. 4. A schematic framework illustrating the roles of core brain areas involved in common and distinct neural networks of S-S and S-R conflicts processing. S-S conflict processing is distinguished by modulation of activity in the left IFC, left SPC, left SOC and right ACC, whereas S-R conflict processing is distinguished by modulation of activity in the left thalamus, right MFC, and right SPC. Common neural networks in S-S and S-R conflict processing include the left SMA/ACC, left MFC, right SPC, and bilateral insula, illustrating that the processing of conflict entails both global (domain-general) and modular (domain-specific) components.

domain-specific and domain-general mechanisms. Our results suggest that resolving conflict involves a hybridized architecture of both modular and centralized cognitive control mechanisms rather than a completely domain-specific or domain-general processor.

Contributions

XL designed and supervised the study. QL and GY made equal contributions to this study, performing the literature search, data extraction and organization and preparing the manuscript. MWC revised the manuscript and provided technical support for data visualization. ZL and YQ participated in performing the literature search and data extraction.

Conflict of interest

None of the authors has a conflict of interest to declare.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.neubiorev.2017.09.032>.

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