



Uncovering cortical activations of discourse comprehension and their overlaps with common large-scale neural networks

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ABSTRACT

We conducted a meta-analysis of 78 task-based functional magnetic resonance imaging (fMRI) studies (1976 total participants) to reveal underlying brain activations and their overlap with large-scale neural networks in the brain during general discourse comprehension and its sub-processes. We found that discourse comprehension involved a neural system consisting of widely distributed brain regions that comprised not only the bilateral perisylvian language zones, but also regions in the superior and medial frontal cortex and the medial temporal lobe. Moreover, this neural system can be categorized into several sub-systems representing various sub-processes of discourse comprehension, with the left inferior frontal gyrus and middle temporal gyrus serving as core regions across all sub-processes. At a large-scale network level, we found that discourse comprehension relied most heavily on the default network, particularly on its dorsal medial subsystem. The pattern associated with large-scale network cooperation varied according to the respective sub-processes required. Our results reveal the functional dissociation within the discourse comprehension neural system and highlight the flexible involvements of large-scale networks.

1. Introduction

Discourse comprehension is central to many facets of human endeavor. Although our capacity to comprehend discourse appears natural to us, from a psycholinguistic perspective, understanding the intended meaning of discourse is a complex task that requires successful processing at many levels (Ferstl, 2010; Ferstl et al., 2008). The underlying mechanisms that enable human brains to accomplish this have been intensively studied for several decades. Advances in neurobiological approaches in the last 20 years, particularly in neuroimaging techniques, have generated new insights to elucidate the neural mechanisms underlying discourse comprehension.

Most early neuroimaging studies of discourse comprehension observed its general processes by comparing discourse processing to a non-discourse processing baseline, such as processing random word lists, unconnected sentences, or reversed speech (e.g., Xu et al., 2005; Yarkoni et al., 2008b). Connected discourses have typically been found to induce greater activation of a wide range of brain regions, including the inferior

frontal gyrus, medial prefrontal cortex, posterior cingulate cortex, angular gyrus, precuneus, anterior temporal lobe, and temporo-parietal junction, than non-discourse baselines (Ferstl et al., 2008; Mar, 2011; Xu et al., 2005). To illustrate, Xu et al. (2005) used fMRI to examine the impact of context, by comparing the comprehension of random word lists, unconnected sentences, and coherent narratives. It was found that the core left-hemisphere perisylvian language areas were always active when engaged in linguistic computations. At the narrative level, the contribution of additional, extra linguistic cognitive processes provoked robust extrasylvian activations in both hemispheres, including precuneus, medial prefrontal cortex, and dorsal temporal-parietal-occipital cortices.

In 2008, Ferstl et al. (2008) presented a quantitative meta-analytic review of text comprehension studies conducted up to 2005. The results revealed an extended language network (ELN) associated with text comprehension processes, which included traditional language areas such as Broca's and Wernicke's areas and several other brain regions, including the anterior temporal lobe, superior temporal sulcus, and

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dorsal medial prefrontal cortex. Mar (2011) also presented a meta-analysis of story comprehension. Story comprehension activated numerous areas, including the bilateral pars orbitalis, temporal pole, post superior temporal sulcus, and temporal-parietal junction, versus a non-story baseline. Active neural clusters were also observed in the left dorsal precentral gyrus, bilateral medial prefrontal cortex, cerebellum, and medial geniculate nucleus extending to the parahippocampal gyrus.

Thus, it is now clear that discourse comprehension as a general process recruits a neural system that not only involves bilateral perisylvian language areas, but also other regions, such as the medial prefrontal cortex and precentral gyrus. Although these results are important, several questions remain unanswered, one of which pertains to functional dissociation within this neural system; specifically, how does this neural system resolve into sub-systems, each of which corresponds to different sub-processes of discourse processing? Moreover, are there core regions that respond to all sub-processes of discourse comprehension?

Recent theoretical and empirical studies have focused on identifying functional dissociation within the neural system associated with language processing. Several studies have proposed neurobiological infrastructural models that could be related to discourse comprehension. The memory, unification, and control model (MUC model) proposed three components of language processing. The first is the memory component, which refers to linguistic knowledge that is encoded and consolidated in memory; this component relies on the temporal cortex, including the angular gyrus in the parietal cortex. The second component is unification (also called integration), which refers to the integration of information stored in memory into larger structures; this requires the contribution of Broca's area and the adjacent cortex in the frontal lobe. The final component is the control component, which associates language with joint action and social interaction via the dorsolateral prefrontal cortex and anterior cingulate cortex (Hagoort, 2013). Similarly, the bilateral activation, integration, and selection (BAIS) model (Jung-Beeman, 2005) also proposed three key components of natural language processing (e.g., processing stories, texts, and conversations): semantic activation in the posterior middle temporal gyrus, semantic integration in the anterior temporal lobes, and semantic selection in the inferior frontal gyrus. Note that these two models were proposed as frameworks to understand general language processing rather than designed explicitly to understand discourse processing. As discourses typically are more complex in structure and meaning than words or sentences, discourse comprehension may involve more neurobiological components than what was proposed in these two models. The MUC model, for instance, does not include the midline regions (e.g., medial prefrontal cortex/precuneus) that are frequently found in studies on discourse comprehension (Whitney et al., 2009; Yarkoni et al., 2008b).

Compared with the MUC and BAIS model, the model of five parallel networks of discourse (Mason and Just, 2006) is more specifically designed to understand discourse processing. It outlines five sub-processes of discourse comprehension: a coarse semantic processing network associated with inference generation (right middle and superior temporal lobes), a coherence-monitoring network that integrates incoherent text (bilateral dorsolateral prefrontal cortex), a text integration network essential for the integration of coherent information (left inferior frontal-left anterior temporal lobe), a protagonist-monitoring network (bilateral medial frontal/posterior right temporal/parietal cortices), and a spatial-imagery network (left dominant, bilateral intra-parietal sulcus).

The above models have significantly expanded our understanding of discourse comprehension. However, they vary substantially in their proposed key processing components and related brain regions. To illustrate, although these models propose integration as an important component of natural language comprehension, the brain areas responsible for integration diverge across models. These differences make it difficult to determine functional dissociation within the neural discourse-processing system.

In addition to theoretical proposals focusing on the sub-processes

underlying discourse processing, numerous recent empirical studies have provided new and divergent findings. The sub-processes considered primarily included inferences, text integration, and pragmatic interpretations. Inference is a process by which perceivers construct propositional meanings from linguistic inputs (Kintsch, 1988). Several studies have examined the inference process by manipulating the degree of connectedness among sentences or the explicitness of expressions. For instance, Kuperberg et al. (2006) required participants to read and make causal coherent judgments of sentences that were either highly causally related, intermediately related, or unrelated to their preceding two-sentence contexts. Contrary to either a highly related or unrelated context, sentences that were intermediately related induced sustained activity increases within left lateral temporal/inferior parietal/prefrontal cortices, right inferior frontal gyrus, and bilateral superior medial prefrontal cortices. Moreover, sentences unrelated to their preceding contexts (in contrast to highly related) were found to induce only transient increases in activity within the right lateral temporal cortex and the right inferior frontal gyrus. These results suggest that, during discourse comprehension, greater effort is needed to understand expressions that are connected, but not closely related. Neural resources underlying inference processing have also been observed in several other areas, including the medial frontal cortex (Friesse et al., 2008), left posterior cingulate cortex (Jang et al., 2013), and right superior temporal gyrus (Virtue et al., 2006).

Integration has also been extensively studied. The classic paradigm for studying the processes underlying integration is to manipulate the consistency of the current information with respect to prior discourse, to ensure that the global context is either relevant or irrelevant for the integration of the current information. Consequently, researchers can elucidate the process underlying integration of inferred propositional meanings of the whole text into a coherent whole (Kintsch, 1988). Regarding consistent expressions, readers can easily relate upcoming words with the context established by prior discourse to smoothly integrate and construct a coherent mental structure of the discourse. Several studies have identified brain regions that support text integration, based on stronger activation in response to consistent text versus inconsistent text (e.g., Egidi and Caramazza, 2013; Ferstl and von Cramon, 2001). These regions included, but were not limited to, the inferior/superior parietal lobule and anterior inferior parietal sulcus (Egidi and Caramazza, 2013), left frontomedian cortex (Ferstl and von Cramon, 2001, 2002), right inferior frontal gyrus (Diaz and Hogstrom, 2011), right temporal pole (Diaz and Hogstrom, 2011), and bilateral fusiform gyrus (Prat et al., 2011). However, for inconsistent expressions, the upcoming information either contradicts or interrupts coherence with the prior discourse context; thus, the current information is not integrated into the prior discourse context. Instead, on detecting inconsistencies, participants try to reconcile breaks in coherence during the process of integration (Egidi and Caramazza, 2013, 2014). This process has also been considered as reflecting integration by some researchers (Ferstl et al., 2005; Mo et al., 2006). Brain regions activated during inconsistent textual integration include the left postcentral gyrus and left superior temporal gyrus (Diaz and Hogstrom, 2011), central insula (Egidi and Caramazza, 2013), right anterior temporal lobe (Ferstl et al., 2005), cerebellum (Mo et al., 2006), and several other brain regions (Hasson et al., 2007; Mo et al., 2006). As both "consistent > inconsistent" and "inconsistent > consistent" contrasts have been interpreted as reflecting the integration process in the literature, here we examined the text integration process with both types of contrast.

An increasing number of studies has also examined the neural substrates involved in pragmatic interpretation during discourse comprehension, by comparing non-literal language processing (e.g., metaphor, irony, sarcasm) with literal language processing (e.g., Diaz and Hogstrom, 2011; Eviatar & Just, 2006; Mashal and Faust, 2010). A wide range of brain regions have been associated with figurative text processing, including the medial prefrontal cortex (Akimoto et al., 2014), left and right inferior frontal gyrus (Bambini et al., 2011), superior

temporal gyrus (Shibata et al., 2010), and left inferior parietal gyri (Rapp et al., 2010). These activations can be modulated by text presentation style (poetic, prosaic; Mashal and Faust, 2010) and discourse congruence (Diaz and Hogstrom, 2011).

Collectively, recent theoretical and empirical studies have suggested possible functional dissociation within the discourse comprehension neural network. However, given that theoretical models differ greatly in their proposed functional subdivisions and that empirical studies have also produced divergent results, understanding of the system remains incomplete. To address this issue, one might summarize findings from the many extant empirical studies; this could directly assist the evaluation and further development of existing theoretical models.

Only one study (Ferstl et al., 2008) has carried out an exploratory meta-analysis of special text processing by considering several sub-processes in a single meta-analytic category (e.g., metaphor task vs. sentence task, inconsistent stories vs. consistent). The results revealed special text processing involved the right anterior temporal lobe and right inferior frontal sulcus (Ferstl et al., 2008). However, as noted by the authors, due to the heterogeneity of the contrasts and the lack of available studies when the meta-analysis was conducted (only 48 foci were used), it was impossible to correlate the results with specific sub-processes of text comprehension (Ferstl et al., 2008). As mentioned above, increasingly many studies have attempted to further specify the underlying neurobiology of the sub-processes of discourse comprehension. Therefore, it is critical to summarize the results regarding the brain regions subserving the sub-processes of discourse comprehension.

Apart from the functional dissociations within the neural system of discourse comprehension, another important question that deserves consideration is how do the brain regions subserving discourse comprehension work at a large-scale network level? A major development in cognitive neuroscience over the previous decade is the development of large-scale network approaches, which provide a framework by which to advance our understanding of divergent brain activations (Bassett and Sporns, 2017; Mason et al., 2007; Yeo et al., 2011). Recently, resting-state fMRI data from 1,000 healthy participants and a data-driven clustering approach enabled researchers to derive seven cortical neuronal networks: visual, somatomotor, dorsal attention, ventral attention, limbic, frontoparietal, and default network (Yeo et al., 2011). This delineation of seven cortical neuronal networks has been used productively in meta-analyses in several fields, including attention-deficit/hyperactivity disorder (ADHD; Cortese et al., 2012), neurotypical aging adults (Li et al., 2015a), and individuals with mild cognitive impairment or Alzheimer's disease (Li et al., 2015b).

Although previous studies have identified many candidate regions that contribute to discourse comprehension, how these brain regions function at a systematic network-level remains largely unknown. To date, a small number of studies have noted the involvement of the default network (Dehghani et al., 2017; Jacobs and Willems, 2018; Tylén et al., 2015) and frontoparietal control network (Aboud et al., 2019) during discourse comprehension, leaving several pertinent questions unanswered. Specifically, how are the default network and the frontoparietal control network weighted during discourse comprehension? Are other networks involved in discourse comprehension? How do the large-scale networks cooperate in discourse comprehension and its sub-processes? Thus, in this study, we aimed to address these questions by combining a large-scale network approach with meta-analytic methods.

Concerning the involvement of large-scale networks, a question related to the contributions of the subsystems within the default network needs to be addressed. An important topic in the field of network neuroscience has been functional fractionation within the default network. Previous studies have identified three functionally distinct subsystems within the default network (Andrews-Hanna et al., 2010; Christoff et al., 2016): the core, the temporal medial, and the dorsal medial subsystem. The core subsystem includes the anterior medial prefrontal cortex, posterior cingulate cortex, and posterior inferior parietal lobule. The temporal medial subsystem includes the hippocampal

formation, parahippocampal cortex, and a number of medial temporal cortical projections, such as the posterior inferior parietal lobule. The dorsal medial subsystem includes the dorsomedial prefrontal cortex, lateral temporal cortex, temporopolar cortex, and parts of the inferior frontal gyrus (Christoff et al., 2016). While this segregation of subsystems is relatively clear, the functions of the subsystems remain controversial, particularly regarding which of these subsystems contribute to memory-based mental construction (Andrews-Hanna et al., 2010; Buckner, et al., 2008; Christoff et al., 2016). Discourse comprehension provides an ideal context within which to study memory-based mental construction (Van den Broek et al., 2005; Zwaan et al., 1995). As previous studies have noted the involvement of the default network in discourse comprehension (Dehghani et al., 2017; Tylén et al., 2015), here we considered the default network subsystems to further reveal their contribution to memory-based mental construction during discourse comprehension.

In summary, our study aimed to complement previous meta-analyses in this field in two important ways. First, we attempted to elucidate functional dissociation within the discourse comprehension neural network. Second, we adopt a large-scale network approach to characterize the involvement of large-scale networks in discourse comprehension. To address these aims, we conducted a meta-analysis of 78 studies. We conducted an overall contrast analysis and a contrast analysis between discourse and nonlinguistic material to reveal the brain regions activated during general discourse comprehension processes. More importantly, we conducted separate contrasts for inference processing, text integration, and pragmatic interpretation, to reveal the processes underlying the activation of identified brain regions and subsystems involved in discourse comprehension. The brain activation results calculated from these contrasts were then used to reveal the involvement of the large-scale neural networks during discourse comprehension.

2. Material and methods

2.1. Study selection

We performed an online search of Web of Knowledge, Pubmed, and Ebsco to find pertinent studies. The search included studies published between January 1980 and Jan 2018. The search terms were “discourse comprehension” OR “narrative comprehension” OR “discourse processing” OR “narrative processing” OR “text comprehension” OR “text processing” OR “context comprehension” OR “context processing” AND “fMRI” OR “neuroimaging” OR “functional magnetic resonance imaging” OR “functional MRI” OR “functional imaging” OR “functional magnetic imaging”. This step yielded 15037 articles. Titles and abstracts from these articles were then screened to isolate fMRI studies that used connected texts (i.e., stimuli that contain more than 1 sentence per trial) as materials and included healthy adult participants. This step yielded 1333 eligible articles. These studies were then carefully reviewed and were included in the meta-analysis if they met the following criteria: (1) used a task-related fMRI method; (2) listed peaks of significant activation in standard stereotactic coordinates (Talairach or MNI space); (3) reported contrasts to enable identification of discourse-relevant activations (e.g., contrast between text and pseudo-word sequences; Friese et al., 2008); (4) performed contrasts for whole-brain analysis; and (5) presented discourses in the participants' native language, and not in a non-proficient second language. This third step yielded 70 eligible articles. To identify as many potential studies as possible, we also conducted an additional literature search using the reference lists cited in the selected studies and a number of relevant review articles (Ferstl, 2010; Ferstl et al., 2008; Mar, 2011). This step yielded an additional six relevant articles, resulting in a final set of 76 articles. Because one article reported data separately for male and female participants (Kansaku et al., 2000) and another article reported two studies (Kurby and Zacks, 2013), altogether 78 studies (from 76 articles) were finally included.

2.2. Quantitative meta-analysis procedures

Two of the current authors (Xiaohong Yang and Xiuping Zhang) independently extracted relevant data from each of the included studies, such as the number of participants, the type of contrasts, types of task, stimuli used in the contrasts, reported foci, and the standard space to which the activation data were normalized. Rare disagreements were discussed and resolved by the authors. Overall, 1727 foci from 78 studies with 1976 participants were included. Detailed information regarding the studies that were included is shown in Table 1.

Activation likelihood estimation (ALE) analysis was implemented using Ginger ALE 2.3.2 (www.brainmap.org). All of the Talairach coordinates were converted into the corresponding MNI coordinates using the “Convert Foci” function in Ginger ALE. A cluster-level family-wise error-corrected threshold of $p < 0.05$ (cluster-forming threshold at voxel-level $p < 0.001$, 5000 permutations) was used for all ALE scores. The resulting ALE images were visualized using BrainNet Viewer (<http://www.nitrc.org/projects/bnv/>; Xia et al., 2013).

To reveal the brain activations during general discourse processing, we conducted two analyses: the overall analysis and the analysis for discourse versus nonlinguistic material. The overall analysis included all the contrasts that we have listed in Table 1. Thus, in the overall analysis, different control conditions were combined, ranging from high-level controls (e.g., literal sentences) to low-level controls (e.g., reversed speech). In our analysis for discourse versus nonlinguistic material, we used a much restricted control condition that included only nonlinguistic materials (e.g., non-words, reversed speech, or letter strings) to discount the low-level processing of visual and auditory signals. Several sub-analyses were conducted to explore the neurobiology underlying the sub-processes of discourse comprehension: inference processing, text integration, and pragmatic interpretation. Contrasts were generated with reference to typical practice in previous studies. Specifically, for the sub-analysis of inference processing, we analyzed “distantly-related/implicit expressions > closely-related/explicit expressions” to reveal significant activations associated with inference processing. Regarding text integration, we analyzed both “consistent expressions > inconsistent expressions” and “inconsistent expressions > consistent expressions” to identify brain regions subserving consistent and inconsistent text integration. We analyzed “non-literal language > literal language” to study pragmatic interpretations.¹

Note that theoretically different types of pragmatic contents (e.g. irony and metaphor) may involve different neuroanatomical underpinnings (Bohrn et al., 2012; Jacobs et al., 2016; Rapp et al., 2012). However, in our analysis of pragmatic interpretations, different types of pragmatic contents were pooled as we were not interested in the neuroanatomy underlying the subtypes of nonliteral language, but in the differences between the three sub-processes of discourse comprehension. It is also worth noting that we did not analyze reading and auditory comprehension separately in the present study. Discourse comprehension could be affected by lower-level processes such as orthographic access or phonological processing (Buchweitz et al., 2009). However, we were more interested in higher-level processes of discourse

¹ We did not create our own classifying criteria to identify the contrasts for the subanalyses. Instead, we followed the frames of the original papers and the classification criteria adopted in prior review papers (Bohrn et al., 2012; Ferstl, 2010; Ferstl et al., 2008; Rapp et al., 2012). The studies that we included in the pragmatic dimension may not explicitly frame the main contrast as “nonliteral > literal language processing”, but they defined their contrasts (e.g., “metaphors vs. non-metaphors” in Bambini et al., 2011) or interpreted the results of their contrasts as revealing either pragmatic, nonliteral, or figurative processing. The term “nonliteral > literal language processing” was only used in our study as an umbrella to cover the various types of contrasts that were related to pragmatic interpretations. The same holds for inference processing. The studies that we included all defined their contrasts or interpreted the results of their contrasts as reflecting inference processing.

comprehension, which are more likely to be shared across modalities (Coderre et al., 2018; Gabriel et al., 2017). Thus, we chose to pool reading and auditory comprehension together.

According to the ALE results, we separately calculated the percentage of significant voxels that overlapped the masks generated for the seven large-scale neural networks (Fig. 3a) proposed by Yeo et al. (2011). In Yeo et al. (2011), seven cortical networks were identified: visual, somatomotor, dorsal attention, ventral attention, limbic, frontoparietal, and default network. Moreover, the cerebellum and striatum were parceled into seven networks based on functional projections of these seven cortical networks (Buckner et al., 2011; Choi et al., 2012). In the present study, the results calculated from the cortical, cerebellar, and striatal networks were then merged. Chi-squared analyses were finally performed to compare the proportions of the networks involved in each contrast. To further explore the involvement of the subsystems within the default network, we delineated this network into the three subsystems proposed by Yeo et al. (2011), i.e., the core, the dorsal medial, and the temporal medial subsystem (Fig. 4a).

2.3. Data and code availability statement

Data can be accessed freely at the OSF website (<https://osf.io/f7yec/quickfiles>).

2.4. Ethics statement

The study was approved by the Review Board of the Institute of Psychology, Chinese Academic of Sciences.

3. Results

3.1. Meta-analysis of the general processes of discourse comprehension

Overall analysis. The activation clusters for the overall analysis (which included all 1727 foci and all contrasts) are presented in Table 2. Discourse comprehension involved many brain regions, including not only perisylvian language regions, but also other areas, such as dorsolateral-dorsomedial frontal regions, caudate, amygdala, and parahippocampal gyri. Both hemispheres showed neural activations. The largest neural cluster was found in the left inferior and middle frontal gyri, which extended to the precentral gyrus. Large clusters were also observed in the bilateral middle temporal gyri, extending to the superior temporal gyri (Fig. 1a).

Discourse versus nonlinguistic material. Fourteen studies reported a total of 223 foci of stronger activation for the processing of discourse material compared with nonlinguistic material. ALE results showed a pattern similar to that derived from the overall analysis (Table 2). Similar to the overall results, activations were bilaterally distributed. The largest clusters were found in the left middle temporal gyri, extending to superior temporal gyri. Similar temporal activations were also noted in the right hemisphere, with activations in the middle temporal gyri extending to both inferior and superior temporal gyri. Large clusters were also found in the left inferior frontal gyri, extending to the middle frontal and superior frontal gyri (Fig. 1b).

3.2. Meta-analysis of the sub-processes of discourse comprehension

Inference processing. Eight studies with 82 foci were used in the contrasts “distantly-related/implicit expressions > closely-related/explicit expressions.” As shown in Fig. 2a and Table 3, the clusters were exclusively found in the left hemisphere. Inference processes were associated with elevated activation in a number of frontal and temporal sites. Frontal activations were found in the inferior frontal gyrus and dorsolateral prefrontal cortex. Temporal activations were localized to the anterior and middle part of the middle temporal gyrus. Activations were also found in the angular gyrus.

Table 1
Characteristics of studies included in the meta-analysis.

Publication	No of subjects	Task	Contrast	No of peaks	Type of contrast
AbdulSabur et al. (2014)	18	listen for comprehension	narrative comprehension > nursery rhyme comprehension	12	
Akimoto et al. (2014)	35	read for intention judgement	irony > incongruity	1	Prag
			irony > literal	2	Prag
Altmann et al. (2014)	24	read for verification	fact > fiction	9	
			fiction > fact	13	
Babajani-Feremi (2017)	429	listen for comprehension	narrative > rest	27	
Bambini et al. (2011)	9	read for familiarity evaluation	metaphors > non-metaphors	10	Prag
Basnakova et al. (2014)	28	listen for comprehension	pooled indirect replies > direct replies	12	Prag
			indirect informative replies > direct replies	5	Prag
			indirect face-saving replies > direct replies	12	Prag
			indirect face-saving replies > indirect informative replies	6	Prag
Basnakova et al. (2015).	20	act as a job interviewer	Indirect > direct	42	Prag
Benelli et al. (2012)	18	read and recall	reading > fixation	12	
			text of high abstraction > text of low abstraction	18	
			text of high emotion > text of low emotion	12	
Bosco et al. (2017)	18	reading for comprehension	deceitful condition > literal condition	4	Prag
			ionic condition > literal condition	6	Prag
			ionic condition > deceitful condition	1	Prag
Caplan and Dapretto (2001)	8	listen for comprehension	reasoning > rest	12	
			topic maintenance > rest	16	
			topic maintenance > reasoning	14	
Choi et al. (2014)	31	read naturally	text > fixation	17	
			text > non word	13	Nonlin
Chow et al. (2008)	19	reading without prediction	predictive and normal reading > pseudoword reading	8	Nonlin
			predictive reading > normal reading	5	Infer
Citron et al. (2016)	24	reading for comprehension	metaphorical stories > literal stories	69	Prag
Cooper et al. (2011)	12	listen for a quiz	story > rest baseline (action)	3	
			story > rest baseline (space)	4	
			story > rest baseline (time)	3	
Crinion and Price (2005)	18	listen for comprehension without explicit task	speech > spectrally reversed speech	20	Nonlin
Diaz and Hogstrom (2011)	16	read for relatedness judgement	metaphor > literal	6	Prag
			congruent > incongruent	10	Con
			incongruent > congruent	3	Incon
Egidi and Caramazza (2013)	14	listen for comprehension	relevant global context > irrelevant global context	1	Con
			irrelevant global context > relevant global context	1	Incon
			locally consistent endings > locally inconsistent endings	13	Con
Egidi and Caramazza (2014)	28	listen for comprehension	congruent > incongruent	3	Con
			incongruent > congruent	7	Incon
Ezzyat and Davachi (2011)	19	read with a surprise recall after reading	boundary sentence > control sentence	2	Incon
Feng et al. (2017)	23	listen for comprehension	pooled indirect replies > direct replies	7	Prag
Ferstl and von Cramon (2001)	12	read for coherence judgement	sentence pairs > letter strings	10	Nonlin
			coherent > incoherent	2	Con
			cohesive > incohesive	2	Con
Ferstl and von Cramon (2002)	9	listen for coherence judgement	sentence pairs > pseudo-sentences	8	Nonlin
			coherent > incoherent	12	Con
Ferstl et al. (2005)	20	listen for consistency judgement	inconsistent > consistent (locked at the target information)	1	Incon
			inconsistent > consistent (from target till end of story)	2	Incon
Friese et al. (2008)	13	read for verification	text > pseudoword sequences	5	Nonlin
			paraphrase > explicit statement	1	Infer
			inference > paraphrase	1	Infer
Guediche et al. (2016)	20	listen for tone detection	related > unrelated	14	Con
			related > same	5	Con
Hartung et al. (2017)	52	listen for comprehension	1st person pronoun > baseline	7	Nonlin
			3rd person pronoun > baseline	3	Nonlin
Hasson et al. (2007)	23	listen for comprehension	text sentences > rest baseline	7	
			(incoherent) more informative sentence > (coherent) less informative sentence	14	Incon
Helder et al. (2017)	31	read for comprehension	incoherent > coherent	28	Incon
Hsu et al. (2015a)	24	read for comprehension	reading > fixation	55	
Hsu et al. (2015b)	33	read for comprehension	supra-natural > control	7	
			supra-natural < control	2	
Jang et al. (2013)	23	read for verification	highly implicit > explicit	11	Infer
			highly implicit > moderately implicit	1	Infer
			highly implicit < explicit	12	
			moderately implicit > explicit	4	Infer
			moderately implicit < explicit	10	

(continued on next page)

Table 1 (continued)

Publication	No of subjects	Task	Contrast	No of peaks	Type of contrast
Jenkins and Mitchell (2010)	15	read for comprehension	mentalizing scenarios > nonsocial scenarios	9	
			ambiguous > unambiguous	1	
			belief > preference	2	
			preference > belief	16	
Jin et al. (2009)	16	read for recognition and comprehension	non-predictive stories > fixation baseline	19	
			predictive stories > fixation baseline	22	
Kandylaki et al. (2015)	20	listen for comprehension	implicit: theory of mind > non theory of mind	16	
			explicit: theory of mind > non theory of mind	1	
Kansaku et al. (2000) (female)	25	listen attentively	story > no voice	4	
			story > reversed speech	2	Nonlin
Kansaku et al. (2000) (male)	22	listen attentively	story > no voice	2	
			story > reversed speech	2	Nonlin
Kuperberg et al. (2006)	15	read for causal coherence judgments	intermediately related > highly related	8	Infer
			intermediately related < highly related	10	
			intermediately related > unrelated	7	Infer
			unrelated > intermediately related	5	
Kurby and Zacks (2013) (study1)	28	read for comprehension	auditory image sentences > low image sentences	13	
			motor image sentences > low image sentences	2	
Kurby and Zacks (2013) (study2)	29	read for comprehension	auditory image sentences > low image sentences	9	
			motor image sentences > low image sentences	1	
Lehne et al. (2015)	23	read for suspense rating	reading > rating	7	
Lillywhite et al. (2010)	20	discourse re-listening task	first presentation > rest	2	
			third presentation > first presentation	3	
Lindenberg and Scheef (2007)	19	read for comprehension	reading > fixation	14	
			reading > letter strings	24	Nonlin
			listening > white noise	20	
			listening > reversed speech	10	Nonlin
Martin-Loeches et al. (2008)	23	reading for comprehension and recall	untitled > title	9	
			title > untitled	13	
Mashal and Faust (2010)	15	read for recognition	text > fixation	17	
Mason and Just (2011)	10	read for comprehension	intentional > control (Sentence 3)	5	Infer
			intentional > control (Sentence 2)	17	Infer
			intentional > fixation (Sentence 2)	9	
			physical > fixation (Sentence 2)	8	
			control > fixation (Sentence 2)	4	
Menenti et al. (2008)	32	read for comprehension	world knowledge violation > world knowledge correct	7	
Miura et al. (2005)	30	read with no explicit task	modern Japanese text > rest	4	
Mo et al. (2006).	12	read for comprehension	inconsistent > consistent	9	Incon
			inconsistent > qualified	14	Incon
Moss et al. (2013)	15	strategy reading	self explanation > reread	19	
			paraphrase > reread	17	
			self explanation > paraphrase	7	
Moss et al. (2011)	21	strategy reading	self explanation > reread	25	
			paraphrase > reread	22	
			self explanation > paraphrase	13	
Nagels et al. (2013)	16	listen for comprehension	similes > control sentence	2	Prag
			control sentence > similes	14	
Nieuwland (2012)	24	read for comprehension	false sentence > true sentence (in counterfactual context)	15	
			false sentence > true sentence (in real world context)	17	
			counterfactual > realworld	6	
Nijhof and Willems (2015).	18	listening only	mentalizing > action	1	
			action > mentalizing	3	
Obert et al. (2014)	19	listen for literal or metaphorical judgement	metaphor > literal	3	Prag
Obert et al. (2016)	21	listen for ironic or literal judgement	irony > literal	8	Prag
O'Sullivan et al. (2015)	24	read for rating	poetic > prosaic	6	
			poetic < prosaic	1	
Prat et al. (2011)	18	read for comprehension	coherent/cohesive > fixation	12	
			coherent/incohesive > fixation	19	
			less-coherent/cohesive > fixation	13	
			less-coherent/incohesive > fixation	7	
			all coherent > all less-coherent	18	Con
			all cohesive > all incohesive	5	Con
			all incohesive > cohesive	3	Incon
Prat et al. (2012).	24	read for comprehension	supporting condition > all context	2	Prag

(continued on next page)

Table 1 (continued)

Publication	No of subjects	Task	Contrast	No of peaks	Type of contrast
Rapp et al. (2010)	15	read and detect a target picture	neutral condition > all context	15	Prag
			opposite condition > all context	12	Prag
			irony > character strings	15	Nonlin
			literal > character strings	6	Nonlin
			Priming > character strings	9	Nonlin
Robertson et al. (2000)	8	read for a recognition test	irony > literal	5	Prag
			sentences with indefinite articles > nonletter character strings	8	Nonlin
			sentences with definite article > nonletter character strings	8	Nonlin
			sentences with definite article > sentences with indefinite articles	2	Con
			sentences with indefinite article > sentences with definite articles	2	Incon
Samur et al. (2015)	20	read for comprehension	figurative > literal	3	Prag
Shibata et al. (2010)	13	read for irony judgement	irony > literal	4	Prag
Shibata et al. (2011)	15	read and judge connotation	indirect reply > literal sentence	10	Prag
Siebörger et al. (2007)	14	listen for coherence judgment	indirect reply condition > fixation baseline	13	
			literal sentence > fixation baseline	9	
			closely related pairs > distantly related pairs	14	
			distantly related pairs > closely related pairs	1	Infer
			distantly related pairs > unrelated pairs	9	Infer
Spotorno et al. (2012)	20	read for comprehension	unrelated pairs > distantly related pairs	3	
			irony > literal	11	Prag
Swett et al. (2013)	17	read and detect a phrase or symbol repetition	passage > non-alphanumeric symbols baseline	17	Nonlin
Tracy et al. (2003)	15	listen for comprehension	central sentences > peripheral sentences	13	
			central sentences > symbol baseline	4	Nonlin
			peripheral sentences > symbol baseline	8	Nonlin
			text only > rest	2	
			coherent > incoherent episodes	9	Con
Tylén et al. (2015)	24	listen for comprehension	incoherent > coherent episodes	12	Incon
			cumulative plot-formation - coherent > incoherent	8	Con
Uchiyama et al. (2006)	20	read for sarcasm judgement	cumulative plot-formation - coherent > baseline	3	
			sarcasm > unconnected	10	Prag
			text > fixation	36	
			implied > explicit (verb point)	1	Infer
			Implied > explicit (coherence break)	2	Infer
Virtue et al. (2008)	26	listen for multiple-choice questions	predictable > explicit	6	Infer
			unpredictable > explicit	3	Infer
			explicit > unpredictable	1	
			stories > unlinked sentences	4	
			irony > literal	4	Prag
Vogeley et al. (2001)	8	read for comprehension	story > rest baseline	10	
Wang et al. (2006)	12	read for comprehension	narrative shifts > baseline (no shifts or boundaries)	8	
Wang et al. (2015)	16	read for comprehension	narrative shifts > random sentence boundaries	3	
Whitney et al. (2009)	16	listen for recall	narratives > letter strings	36	Nonlin
Xu et al. (2005)	22	read for comprehension	narrative > words	29	
			narrative > sentences	17	
			story outcome > story onset	9	
			reading > fixation	21	
			story > rest baseline	11	
Yarkoni et al. (2008a)	28	read for comprehension	story > scramble sentences	11	
Yarkoni et al. (2008b)	25	read for comprehension and memory test			

Note. Nonlin: Discourse vs. Nonlinguistic material; Infer: Inference processing; Con: Consistent vs. Inconsistent; Incon: Inconsistent vs. consistent; Prag: Pragmatic interpretations.

Text integration. Nine studies with 104 foci reported activations for the “consistent expressions > inconsistent expressions” contrast. Clusters were exclusively found in the left hemisphere (Fig. 2b, Table 3). The most observable clusters were the left inferior frontal gyrus and the left middle temporal gyrus. Ten studies with 96 foci reported stronger activation for the “inconsistent expressions > consistent expressions” contrast. Several regions were found, including the left inferior frontal gyrus, left dorsal medial prefrontal cortex, posterior part of the left middle temporal gyrus, and the right lingual gyrus (Fig. 2c, Table 3).

Pragmatic interpretations. Nineteen studies with 271 foci reported activation for the “non-literal language > literal language” contrast. Non-literal language processing elicited stronger activations in bilateral inferior frontal gyri and dorsal medial prefrontal cortex. Large clusters were also found in bilateral middle and superior temporal gyri (Fig. 2d, Table 3).

3.3. Computation of neuronal networks

3.3.1. Involvement of the seven large-scale networks

We calculated the percentage of significant voxels located in each of the seven neuronal network parcellations of the human brain (Fig. 3b). The overall analysis revealed that discourse comprehension relied primarily on the default network (73.8%). Activations were also found in other networks, including the frontoparietal network (12.9%), ventral attention network (4.5%), dorsal attention network (1.9%), somatomotor network (6.8%), and limbic network (0.1%). Network computations for discourse and nonlinguistic material revealed a pattern similar to the overall analysis. Activations were again primarily noted in the default network (69.7%). Other activations were observed in the frontoparietal network (8%), ventral attention network (8%), dorsal attention network (3.2%), visual network (4.5%), somatomotor network (6.6%), and limbic network (0.1%).

Table 2
Regional activations for the general process of discourse comprehension.

cluster	Volume	Weighted Center (X,Y,Z)			Extrema Value	Maximum ALE value (X,Y,Z)			BA	Anatomical Label
<i>Overall analysis</i>										
1	19784	-48.42	22.17	12.24	0.087	-50	28	-4	47	Inferior Frontal Gyrus
					0.065	-52	24	10	45	Inferior Frontal Gyrus
					0.061	-46	14	24	9	Inferior Frontal Gyrus
					0.057	-46	6	50	6	Precentral Gyrus
					0.037	-48	20	38	8	Middle Frontal Gyrus
					0.031	-42	44	-14	47	Middle Frontal Gyrus
					0.026	-36	16	-18	47	Inferior Frontal Gyrus
0				0.026	-34	18	-14	47	Inferior Frontal Gyrus	
2	17448	-55.63	-30	-1.95	0.075	-56	-36	0		Middle Temporal Gyrus
					0.054	-56	-12	-12	21	Middle Temporal Gyrus
					0.050	-56	-54	12	39	Superior Temporal Gyrus
					0.043	-52	6	-22	21	Middle Temporal Gyrus
					0.043	-56	-10	-20	21	Middle Temporal Gyrus
					0.040	-52	0	-24	21	Middle Temporal Gyrus
					0.037	-56	-56	26	39	Superior Temporal Gyrus
3	10800	-4.6	42.96	41.24	0.029	-58	-20	4	41	Superior Temporal Gyrus
					0.054	-8	56	34	8	Superior Frontal Gyrus
					0.047	-4	48	42	8	Superior Frontal Gyrus
					0.038	-14	58	24	9	Superior Frontal Gyrus
					0.035	-6	36	44	8	Medial Frontal Gyrus
					0.035	-4	16	60	6	Superior Frontal Gyrus
									0.035	-2
4	10760	55.77	-18.75	-9.47	0.031	-8	32	56	6	Superior Frontal Gyrus
					0.030	-8	24	54	8	Superior Frontal Gyrus
					0.030	8	58	26	9	Superior Frontal Gyrus
					0.056	54	-30	-4	21	Middle Temporal Gyrus
					0.055	56	-34	-10	21	Middle Temporal Gyrus
					0.052	58	-20	2	41	Superior Temporal Gyrus
					0.048	54	6	-22	21	Middle Temporal Gyrus
5	4208	54.88	28.36	2.05	0.035	56	-8	-10	22	Superior Temporal Gyrus
					0.054	56	32	-2	45	Inferior Frontal Gyrus
					0.043	58	26	18	9	Inferior Frontal Gyrus
6	1544	57.98	-57.11	25.49	0.035	46	28	-14	47	Inferior Frontal Gyrus
					0.048	58	-58	26	39	Superior Temporal Gyrus
7	1400	-46.02	-67.13	28.61	0.038	-46	-70	30	39	Middle Temporal Gyrus
					0.027	-44	-58	26	39	Middle Temporal Gyrus
8	1080	-10.3	7.25	11.16	0.045	-10	8	10		Caudate
9	920	-27.1	-8.87	-20.05	0.034	-32	-10	-22		amygdala
					0.032	-24	-6	-20		amygdala
10	496	-24.62	-25.92	-7.73	0.032	-24	-28	-8	28	Parahippocampal Gyrus
11	424	11.13	6.01	10.73	0.035	10	6	10		Caudate
12	368	23.15	-7.42	-19.05	0.032	22	-8	-18		amygdala
<i>Discourse vs. Nonlinguistic material</i>										
1	4208	-57.93	-43.07	5.78	0.029	-56	-36	2	22	Middle Temporal Gyrus
					0.021	-62	-46	10	22	Superior Temporal Gyrus
2	2160	-56.94	-5.98	-18.2	0.019	-58	-12	-14	21	Middle Temporal Gyrus
					0.014	-60	6	-26	21	Middle Temporal Gyrus
					0.014	-56	-8	-22	21	Middle Temporal Gyrus
					0.014	-56	2	-20	21	Middle Temporal Gyrus
3	1536	-46.45	5.57	50.64	0.025	-46	6	52	6	Middle Frontal Gyrus
4	1432	-52.66	25.32	15.02	0.020	-48	26	16	46	Middle Frontal Gyrus
5	1360	54.32	-34.78	-6.86	0.018	54	-34	-6	21	Middle Temporal Gyrus
6	1000	-7.99	53.32	39.71	0.018	-8	54	36	8	Superior Frontal Gyrus
					0.018	-6	52	46	8	Superior Frontal Gyrus
7	864	57.16	-4.02	-24.8	0.016	58	-8	-26	20	Inferior Temporal Gyrus
					0.012	52	8	-20	38	Superior Temporal Gyrus
					0.011	58	0	-22	21	Middle Temporal Gyrus
8	712	-27.04	-22.58	-9.92	0.018	-28	-22	-10		Hippocampus
9	552	53.42	31.34	-5.69	0.017	52	32	-6	45	Inferior Frontal Gyrus
10	552	-1.31	-71.66	13.7	0.021	-2	-72	14	30	Cuneus
11	488	-57.54	28.51	-2.76	0.014	-60	28	-8	47	Inferior Frontal Gyrus
					0.013	-58	30	-2	45	Inferior Frontal Gyrus
					0.011	-52	26	0	45	Inferior Frontal Gyrus

Regarding the sub-processes of discourse comprehension, network computations for inference processes revealed activations predominately in the default network (79%) and frontoparietal network (20.9%). Additional activation was also found in the limbic network (0.1%). For

text integration, activations for the contrast “consistent expressions > inconsistent expressions” were predominately found in the default network (88.4%), with additional activations in the frontoparietal network (11.6%). Activations for the contrast “inconsistent

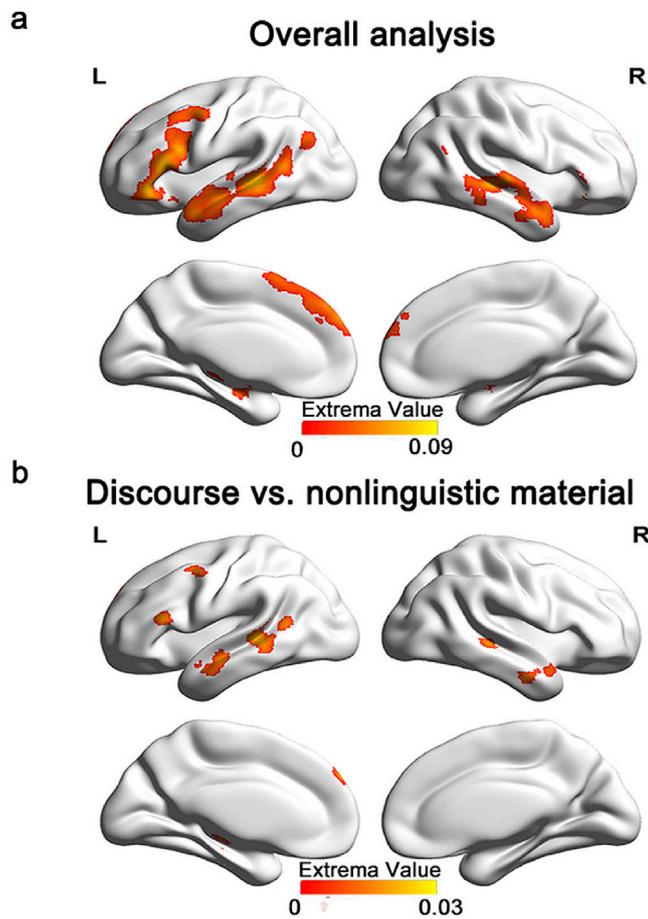


Fig. 1. Regions involved in general discourse processing. L: left hemisphere; R: right hemisphere.

expressions > consistent expressions” were found in the default network (62.1%), frontoparietal network (1%), ventral attention network (17.3%), dorsal attention network (1.3%), visual network (7%), and somatomotor network (11.3%). Pragmatic interpretations demonstrated activations almost exclusively in the default network (91.1%). Additional activations were located in the frontoparietal network (3.7%), limbic network (1%), ventral attention network (0.6%), dorsal attention network (0.8%), and somatomotor network (2.8%).

Chi-squared analyses revealed that these sub-processes differed significantly in the proportions of the networks recruited ($\chi^2 = 128$, $p < .001$). Pairwise comparisons (Bonferroni corrected; adjusted significance level, $p = .05/6 = 0.008$, for the six inter-group comparisons) were then performed to determine statistical differences between the sub-processes. All comparisons were significantly different (all χ^2 s > 18.4, all $ps < .002$), except for the comparison between pragmatic interpretations and consistent text integration ($\chi^2 = 10.05$, $p = .07$) and that between inference processing and consistent text integration ($\chi^2 = 2.94$, $p = .23$). To assess whether these sub-processes differed significantly from the general processes of discourse comprehension, we also compared the network results of each sub-process with those of discourse vs. nonlinguistic material (adjusted significance level, $p = .05/4 = 0.013$, for the four inter-group comparisons). The proportions of networks recruited in other sub-processes were different from those found in the general processes of discourse comprehension (inference processing, consistent discourse integration, and pragmatic processing, all χ^2 s > 18.12, all $ps < .01$), except for inconsistent discourse integration ($\chi^2 = 11.37$, $p = .08$).

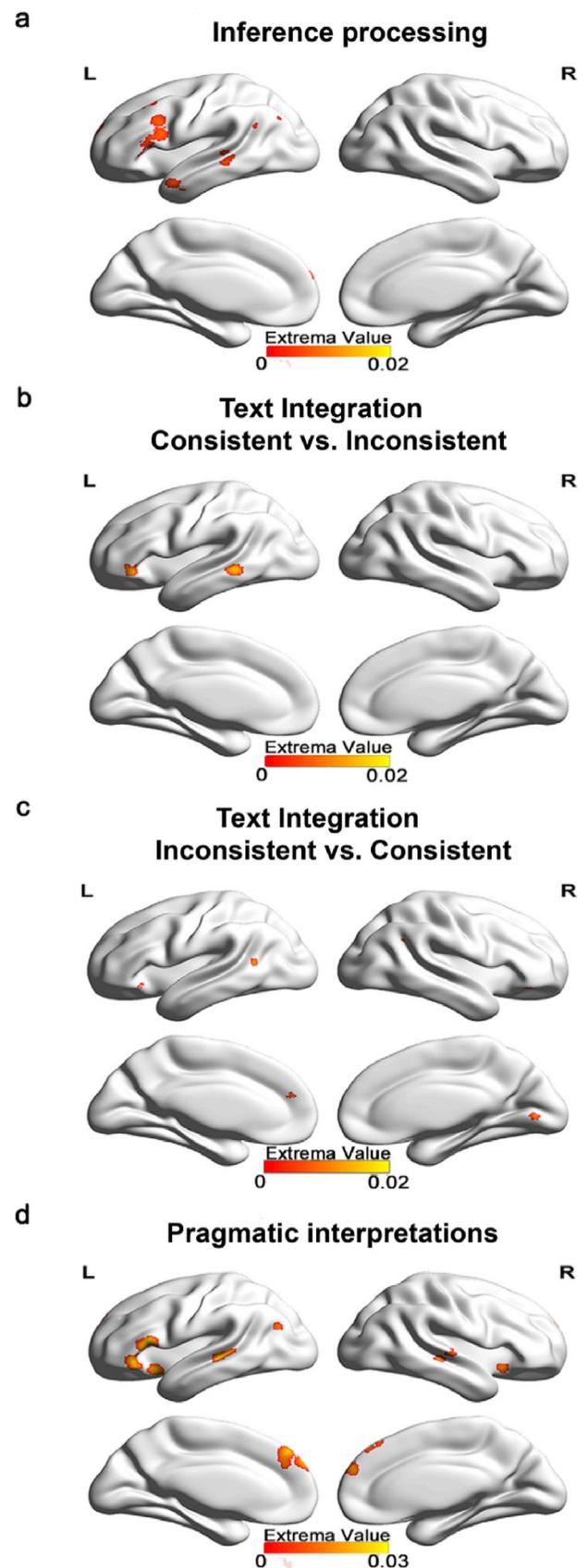


Fig. 2. Regions involved in the sub-processes of discourse comprehension. L: left hemisphere; R: right hemisphere.

Table 3
Regional activations for the sub-processes of discourse comprehension.

cluster	Volume	Weighted Center (X,Y,Z)			Extrema Value	Maximum ALE value (X,Y,Z)			BA	Anatomical Label
Inference processing										
1	3400	-48.24	20.44	15.24	0.016	-48	14	26	9	Inferior Frontal Gyrus
					0.015	-50	28	-4	47	Inferior Frontal Gyrus
					0.014	-48	20	14	45	Inferior Frontal Gyrus
					0.009	-58	22	20	9	Inferior Frontal Gyrus
2	960	-57.23	-33.63	-2.91	0.014	-58	-34	-6	21	Middle Temporal Gyrus
					0.012	-56	-34	2	22	Middle Temporal Gyrus
3	872	-13.97	58.81	23.29	0.020	-14	58	24	9	Superior Frontal Gyrus
4	776	-50.55	3.14	-25.92	0.013	-52	0	-26	21	Middle Temporal Gyrus
					0.013	-50	6	-24	38	Middle Temporal Gyrus
5	408	-47.56	-73.97	33.16	0.013	-48	-74	32	39	Middle Temporal Gyrus
6	344	-34.28	20.3	45.22	0.010	-34	20	46	6	Middle Frontal Gyrus
7	336	-37.71	-79.31	40.88	0.013	-38	-80	42	19	Superior Occipital Gyrus
8	288	-45.27	-56.89	28	0.010	-46	-56	28	39	Superior Temporal Gyrus
					0.009	-44	-62	28	39	Middle Temporal Gyrus
Text integration: consistent vs. inconsistent										
1	712	-60.34	-39.15	-5.66	0.016	-60	-40	-6	21	Middle Temporal Gyrus
2	672	-48.21	35.61	-5.28	0.013	-48	36	-6	47	Inferior Frontal Gyrus
3	328	-47.37	23.23	40.06	0.013	-48	24	40	8	Middle Frontal Gyrus
Text integration: inconsistent vs. consistent										
1	456	60.02	-54.28	29.93	0.015	62	-54	30	40	Supramarginal Gyrus
					0.009	52	-54	30	39	Superior Temporal Gyrus
2	440	39.73	37.83	-13.01	0.016	40	38	-12	47	Inferior Frontal Gyrus
3	432	-54.27	-56.3	9.51	0.012	-56	-58	12	39	Middle Temporal Gyrus
					0.010	-52	-54	4	37	Middle Temporal Gyrus
4	416	-42.45	24.38	-12.63	0.014	-42	24	-12	47	Inferior Frontal Gyrus
5	280	-11.46	45.67	20.64	0.012	-12	46	20	9	Medial Frontal Gyrus
6	272	44.01	-18.56	8.68	0.012	44	-18	8	13	Insula
7	192	-1.18	-15.82	39.83	0.010	-2	-16	40	24	Cingulate Gyrus
8	168	5.97	-77.16	1.81	0.011	6	-78	2	18	Lingual Gyrus
Pragmatic interpretations										
1	5112	-1.54	49.54	34.65	0.023	-4	44	42	8	Superior Frontal Gyrus
					0.022	-6	58	32	9	Medial Frontal Gyrus
					0.020	6	56	28	9	Superior Frontal Gyrus
					0.018	-2	40	34	6	Medial Frontal Gyrus
					0.014	4	36	50	8	Superior Frontal Gyrus
2	4936	-50.1	26.12	-0.54	0.012	4	50	16	9	Medial Frontal Gyrus
					0.027	-56	22	12	45	Inferior Frontal Gyrus
					0.026	-52	22	8	45	Inferior Frontal Gyrus
					0.026	-48	32	-6	45	Inferior Frontal Gyrus
					0.020	-46	32	-12	47	Inferior Frontal Gyrus
					0.019	-54	22	-8	47	Inferior Frontal Gyrus
3	1928	-50.41	-32.15	-0.31	0.022	-52	-30	-2	22	Superior Temporal Gyrus
4	1192	-35.33	16.53	-15.92	0.026	-36	16	-18	47	Inferior Frontal Gyrus
					0.024	-34	16	-14	13	Extra-Nuclear
5	432	35.82	19.74	-11.78	0.017	34	20	-12	13	Insula
6	424	-55.31	-57.34	37.63	0.019	-56	-58	38	40	Supramarginal Gyrus
7	384	51.62	-26.91	-4.97	0.017	52	-28	-6	21	Sub-Gyral
8	376	61.1	-20.91	-2.42	0.014	64	-22	-6	21	Middle Temporal Gyrus
					0.013	60	-20	0		Superior Temporal Gyrus
9	336	45.46	27.57	-15.39	0.016	46	28	-14	47	Inferior Frontal Gyrus
10	304	-42.66	-70.69	24.62	0.015	-44	-70	26	39	Middle Temporal Gyrus

3.3.2. Functional dissociation within the default network

Results for the subsystems of the default network are shown in Fig. 4b. Note that the dorsal medial subsystem contributed significantly to the default network activation versus the other two subsystems. Activation of the dorsal medial subsystem in the overall analysis and the analysis comparing discourse and nonlinguistic material occurred in 90.1% and 96% of comparisons, respectively; these percentages outweighed those for the other two subsystems. Regarding the sub-processes of discourse comprehension, the dominant role of the dorsal medial subsystem was observed again, as evidenced by the extremely high proportion of activation in the analysis of consistent discourse integration (approximately 100% for the dorsal medial subsystem). The proportion of activation for the core subsystem reached 41.5% for

inconsistent text integration.

Chi-squared analyses revealed that these sub-processes differed significantly in the proportions of activated default network subsystems ($\chi^2 = 83.01, p < .001$). Further pairwise comparisons (adjusted significance level, $p = .05/6 = 0.008$, for the six inter-group comparisons) revealed significant differences between inference processing and consistent discourse integration, inference processing and inconsistent discourse processing, consistent discourse integration and inconsistent discourse integration, and between inconsistent text integration and pragmatic interpretations ($\chi^2_s > 17.39, ps < .008$). No other comparisons were significant ($\chi^2_s < 7.18$). To assess whether these sub-processes differed significantly from the general processes of discourse comprehension, we also compared the default network subsystem results for

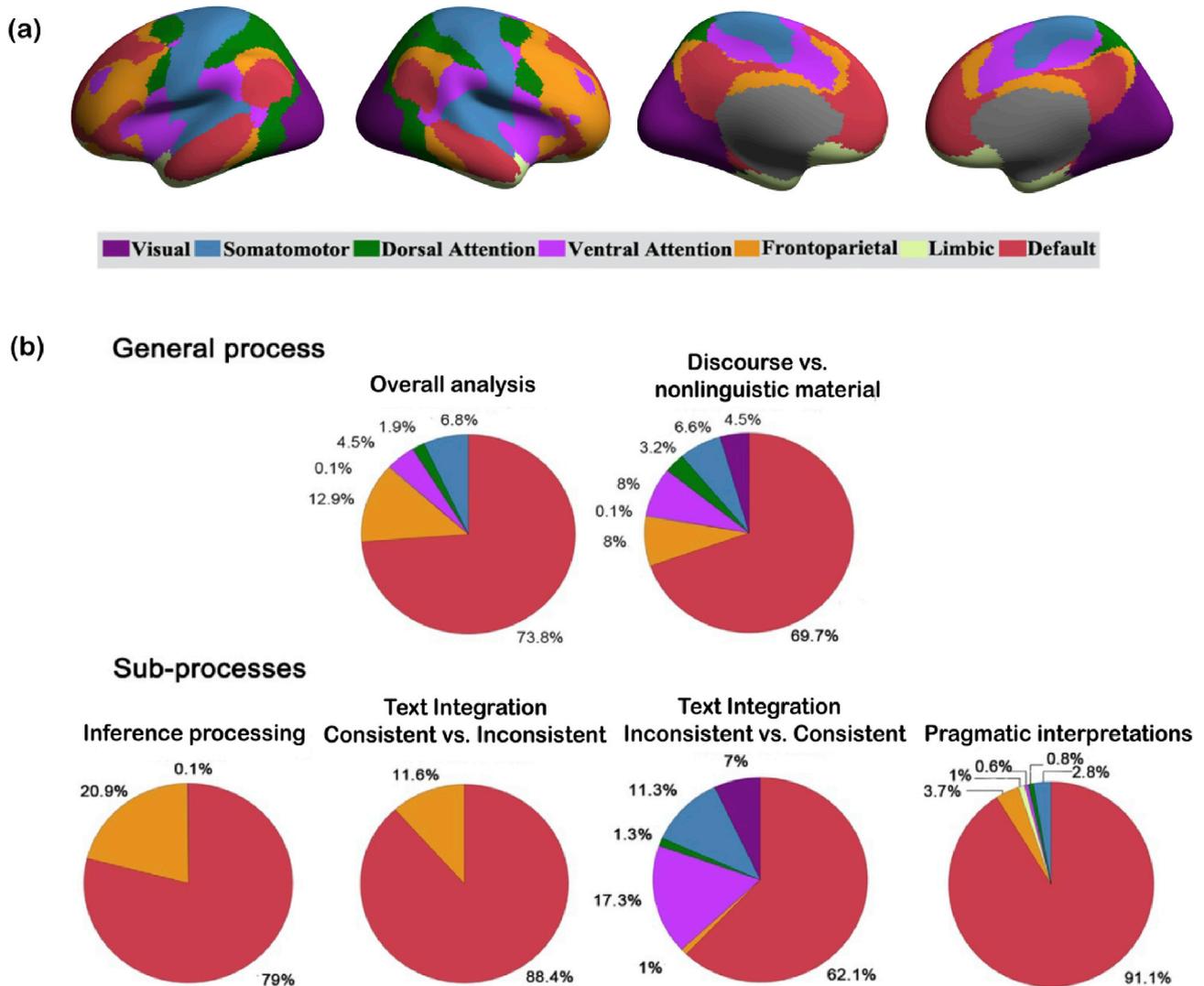


Fig. 3. (A) The seven large-scale networks and (b) proportions of activations that were located in the seven large-scale networks during general discourse processing and its sub-processes.

each sub-process with those of discourse vs. nonlinguistic contrast (adjusted significance level, $p = .05/4 = 0.013$, for the four inter-group comparisons). The results revealed that inconsistent discourse integration differed significantly from general discourse processing in terms of the default network subsystems activated ($\chi^2s > 40.22$, $ps < .001$). No other comparisons were significant ($\chi^2s < 8.17$, $ps > .013$).

4. Discussion

Here, we explored the brain activations associated with general discourse comprehension and its sub-processes. Further, we explored the large-scale neuronal networks underlying these processes. Several noteworthy findings were observed. First, discourse comprehension in general involved a widely distributed network of brain regions; however, these regions were grouped into functional sub-systems associated with different sub-processes of discourse comprehension. Second, the left inferior frontal and middle temporal gyri were the core regions across all sub-processes. Third, the default network, particularly its dorsal medial subsystem, was most heavily weighted during discourse comprehension, cooperating with other networks to establish successful comprehension. Finally, the pattern of large-scale network recruitment varied according to the type of sub-process. These findings extend the extant results and

have significant implications for understanding the neurobiology of discourse comprehension, which we discuss below.

4.1. Regional activations: the neural system of discourse comprehension and its functional division

4.1.1. The general process of discourse comprehension

The overall meta-analysis clearly demonstrated that discourse processing involved an extended network of regions of the brain, including bilateral inferior frontal gyri; left middle frontal gyrus; bilateral dorsal medial prefrontal cortex, from the temporal pole, extending caudally to the angular gyrus; and bilateral parahippocampal gyri. In a more fine-grained analysis comparing discourse comprehension processing to the processing of non-linguistic material, frontal and temporal activations reappeared, along with activations in the middle and superior frontal regions. This is consistent with many previous studies which showed that discourse comprehension relied on a wide range of brain regions, including lateral prefrontal cortex, anterior-posterior temporal lobe, and medial wall of the left hemisphere (Ferstl et al., 2008; Mar, 2011; Yang et al., 2018).

Although an extended network of brain regions was found to support the general processes of discourse comprehension, only the left inferior

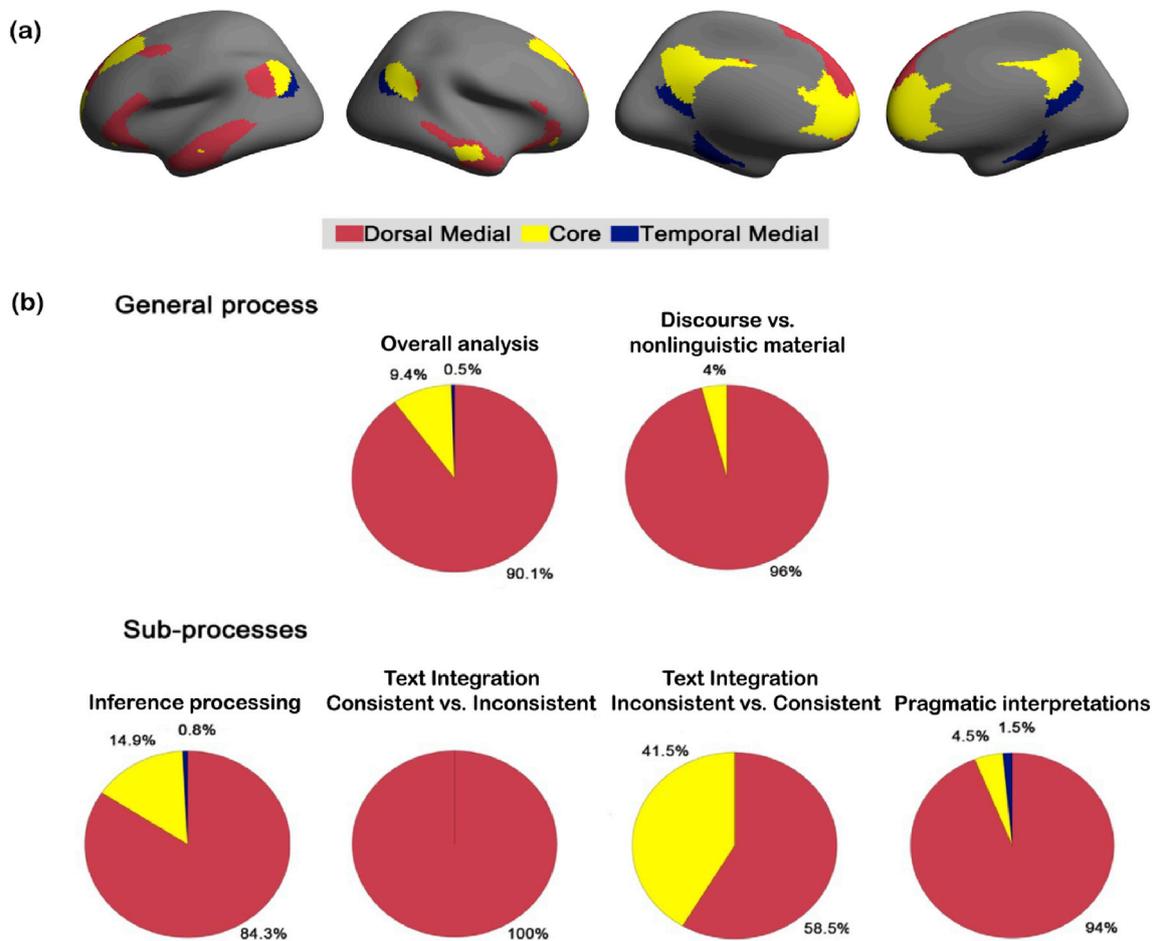


Fig. 4. (A) The subsystems of the default network and (b) proportions of activations that were located in the subsystems of the default network during general discourse processing and its sub-processes.

frontal gyrus and left middle temporal gyrus were consistently activated across all sub-processes of discourse comprehension. Thus, we speculate that these are the core regions supporting discourse processing. In particular, we suggest that these regions support high-level operations at the discourse level, rather than operations on words or sentences. Previous models have proposed different functions for these two regions during language comprehension (Hagoort, 2013; Jung-Beeman, 2005; Mason and Just, 2006). However, our findings compare more favorably with the five parallel networks of discourse comprehension model (Mason and Just, 2006); the left inferior frontal and left temporal areas function in cooperation as a text-integration network that integrates coherent information.

4.1.2. Functional division within the neural system of discourse comprehension

We conducted separate contrasts for different sub-processes of discourse comprehension and thereby revealed that the neural discourse comprehension system is grouped into sub-systems corresponding to their respective sub-processes. This provides evidence that the neural discourse comprehension system is consisting of multiple subsystems, each of which is differentially involved with different aspects of high-level cognitive processing.

Apart from activations in the left inferior frontal gyrus and left middle temporal gyrus, inference processing was also found to activate the dorsolateral prefrontal cortex and angular gyrus. The functional role of the dorsolateral prefrontal cortex in inference processing could be to sustain and evaluate the coherence of strategic inferences with respect to the described situation (Chow et al., 2008). In contrast, the role of the

angular gyrus may be to process semantic information by integrating input information with prior knowledge (Jang et al., 2013).

Regarding text integration, consistent and inconsistent text integration activated significantly distinct brain networks. Consistent text integration primarily relied on two core regions: the left inferior frontal gyrus and left middle temporal gyrus. This system may ensure consistent integration of textual information into mental representations without considerable cognitive effort. Compared to consistent text integration, inconsistent text integration activated an additional set of regions, including the left dorsal medial prefrontal cortex and right lingual gyrus. The dorsal medial prefrontal activations may reflect non-automatic cognitive processes subserving the integration between external stimulation and idiosyncratic response criteria (Siebörger et al., 2007). The right lingual gyrus is active during conflict processing (Wittfoth et al., 2006). Thus, activations of this region may reflect the cognitive effort needed to resolve inconsistencies during discourse processing.

The most notable distinction between pragmatic activations and other sub-processes is that pragmatic interpretations resulted in substantial dorsal medial prefrontal activations. Dorsal medial prefrontal activations have been repeatedly noted in tasks that involve inference of others' mental states (i.e., theory of mind; Mason and Just, 2011) and social cognition (Forbes and Grafman, 2010). In line with the literature, the heavy reliance of pragmatic interpretations on dorsal medial prefrontal activations may be because pragmatic interpretations place great demands on the need to filter relevant aspects of context and infer the intentions of other people (Bambini et al., 2011).

One notable absence in our results is that discourse comprehension did not activate the precuneus across all our analyses. This contradicts

with previous findings that suggest a crucial role of the precuneus in coherence building during discourse comprehension (Helder et al., 2017; Whitney et al., 2009; Zacks and Ferstl, 2016). However, the absence of precuneus should not come as a surprise given that in a previous ALE meta-analysis on narrative comprehension (Mar, 2011), significant clusters on midline areas were only found in medial prefrontal areas but not precuneus. It may be that the activations of precuneus are content dependent. Speer et al. (2009) found that changes in character, time, objects, and goals engaged activations in the precuneus while changes in causal or spatial changes did not, suggesting that the engagement of this region may depend on story content. Other studies have noted that the precuneus is largely involved in the integration of self-related mental imagery contents and episodic memory retrieval (Cavanna and Trimble, 2006; Rikandi et al., 2016). Thus, the precuneus may selectively support story contents that are highly demanding of self-related imaginary or retrieval of episodic memories.

4.2. Large-scale network activations

4.2.1. The general process of discourse comprehension

The overall analysis showed that discourse comprehension primarily relied on activation of the default, ventral attention, and somatomotor networks. However, when comparing discourse processing to processing non-linguistic material, this pattern reappeared, demonstrating that large-scale networks do not function in isolation to support discourse comprehension; rather, they function through cooperation with other networks in support of discourse processing.

Among all networks, the default network was central and most pervasively related to discourse comprehension. It represented the largest portion of network activation for the general process of discourse comprehension and was engaged during all sub-processes of discourse comprehension. Only a small number of studies of discourse processing have noted the importance of the default network (Dehghani et al., 2017; Lin et al., 2018; Tylén et al., 2015). In our study, by providing direct evidence from computations of large-scale network recruitment, we demonstrated that the default network is the core of discourse comprehension.

In previous studies, the default network has been associated with social cognition (Spreng and Andrews-Hanna, 2015), affective processing (Amft et al., 2015), and word-level concept processing (Binder et al., 2009). Thus, involvement of the default network during discourse comprehension may indicate that processing social, affective, and conceptual information related to discourses recruited the default network. However, discourse comprehension does not include only these aspects. It is a process that necessitates building a mental representation, which involves co-activation of concepts in memory to create a cohort of related ideas and thereby represent the situation in spatial, temporal, causal, protagonist, and social terms (Van den Broek et al., 2005; Zwaan et al., 1995). Thus, the heavy weighting of the default network during discourse comprehension could also be an indication that this network plays a more general role in constructing mental representations.

By further collapsing activation of the default network into its three subsystems, we showed that activations of the default network were located largely in its dorsal medial subsystem. This suggests that, of the three subsystems, the dorsal medial subsystem is most closely related to the development of mental representations. This provides insight into the divergent functions of the three subsystems within the default network. These findings regarding the default network, in particular its dorsal medial subsystem, have important implications for the ongoing debate about the functional significance of the default network; we discuss this in more detail in section 4.4.

4.2.2. Sub-processes of discourse comprehension

Sub-processes recruited the default, frontoparietal, and ventral attention networks to a greater extent than other networks. Of the sub-processes examined, consistent text integration and pragmatic

interpretation relied substantially on the default network (i.e., 88.4% and 91.1%, of the activation proportions respectively), suggesting that the default network not only supports the construction of mental representations, but also supports the processing of others' intentions during discourse comprehension. However, for inference processing and inconsistent text integration, the percentages of activations found in other networks increased to 21% and 37.9%, respectively. This provides evidence that the pattern of network co-activation varies with the sub-processes of discourse comprehension.

The sub-processes, including inference processing and consistent text integration, most extensively relied upon cooperation between the default network and the frontoparietal network. The frontoparietal network is a cognitive and action control network that is commonly engaged during effortful cognitive task performance requiring information or rules to be held in mind (Kozioł et al., 2014). Thus, the functional role of the frontoparietal network during inference processing and consistent text integration could be a top-down control system that helps to generate internal inferences and mental representations in the face of disruption by external information. Recently, it has been argued that cooperation between the default network and the frontoparietal network supports the production of an internal train of thought (Smallwood et al., 2012). Our results that inference processing and consistent text integration involved the default network and the frontoparietal network are consistent with this view and provide further evidence for the function of the cooperation between these networks.

Compared with other sub-processes, inconsistent text integration discourse activated a larger proportion of the ventral attention network. The ventral attention network has been assumed to be involved in stimulus-driven attentional control (Vossel et al., 2012) and to respond when behaviorally relevant objects are detected (Corbetta et al., 2008). Thus, involvement of the ventral attention network during discourse comprehension may reflect perceivers detecting important and relevant discourse content. A recent study proposed that the ventral attention network and the default network can interact and transform into an "action control" network to guide attention (Njiokiktjien et al., 2010). Thus, cooperation between the default network and ventral attention network may indicate that perceivers initiate an attention-control process when they encounter inconsistencies during discourse processing. Inconsistent text integration also recruited a larger portion of the somatomotor network, which is consistent with a previous study that suggested the somatomotor network generates automated behaviors recruited for quick responses (Kozioł et al., 2014).

We found changes in the sub-systems of the default network involved in sub-processes of discourse comprehension. Compared with consistent text integration, recruitment of the dorsal medial subsystem decreased, while recruitment of the core subsystem increased during inference processing and inconsistent text integration. Note that inference processing and inconsistent text integration involve more cognitive control in order to process linguistic materials in discourse comprehension. Thus, this change in the pattern of activity within the default network compares favorably with the proposed functional dissociation within the default network. That is, the dorsal medial subsystem subserves mentalizing, conceptual processing, and emotional processing, while the core subsystem subserves internally goal-oriented cognition (Christoff et al., 2016). As inference processing also involved the frontoparietal network and inconsistent text integration involved the ventral attention network, it could be argued that, during the effortful cognitive processing of discourse materials, greater recruitment of goal-oriented networks occurs to support the task demands; this is observed both among and within networks.

4.3. Implications for existing neurocognitive models of discourse comprehension

As mentioned earlier, over recent decades, several neurocognitive models have been proposed that identify the key cognitive components

involved in language comprehension. Such models include the memory, unification, and control (MUC) model (Hagoort, 2013); the bilateral activation, integration, and selection (BAIS) model (Jung-Beeman, 2005); and the model of five parallel networks of discourse (Mason and Just, 2006). These models differ greatly in their proposed key cognitive components and related neural anatomy. For instance, integration in the MUC model is referred to as the unification component; it recruits frontal areas, including Broca's area and adjacent cortex. In the BAIS model, integration is supported by regions in anterior middle/superior temporal gyri. In the model of five parallel networks of discourse, a dichotomous classification of integration is proposed, with coherent information integration supported by the left inferior frontal/anterior temporal regions and incoherent text integration supported by bilateral dorsolateral prefrontal regions.

In the current study, ALE results showed that coherent text integration predominately recruited the left inferior frontal gyrus and left middle temporal gyrus, while incoherent text integration recruited other areas, including the left dorsal medial prefrontal cortex and right lingual gyrus. These results concur with the model of five parallel networks of discourse rather than the other two models, as both left inferior frontal and middle temporal gyrus are important regions for integration in this model. Furthermore, our results showed that coherent and incoherent text integration differed substantially in the regions recruited, which also substantiate the dichotomy of integration proposed in the model of five parallel networks of discourse.

Although our brain-region findings support the model of five parallel networks of discourse to a greater extent than the other two models, the functional regions obtained in our analysis also differed substantially from the former model in many aspects. For instance, inference processing is supported by the coarse semantic network in the right middle and superior temporal regions in this model. However, our meta-analysis of inference processing revealed activations exclusively in the left hemisphere, encompassing the inferior frontal gyrus, dorsolateral prefrontal cortex, anterior and middle part of the middle temporal gyrus, and angular gyrus.

The divergence in brain regions between the current findings and those proposed in previous neurobiological models requires further attention. A possible explanation is that these models were proposed several years ago; as more studies have been conducted, divergent results have occurred. Thus, future models should incorporate recent findings and further specify the cognitive functions of the key brain areas underlying discourse comprehension.

Another aspect of our findings that should be considered for neurocognitive models is cooperation between the default network and control/attention networks. While most existing theories have noted the involvement of control or attention components in discourse processing, only one (i.e., the MUC model) adopted a dynamic network view, in which the core language-processing regions must interact with other networks (e.g., attentional networks) to establish full functionality of language and communication (Hagoort, 2014). However, this model does not specify the core networks of language processing nor the specific attentional networks involved. By analyzing brain activations at the large-scale network level, we showed that discourse comprehension requires cooperation among different high-level neural systems. Specifically, discourse comprehension requires (1) substantial involvement of the default network (particularly its dorsal medial subsystem) and (2) coupling of default network activity with goal-directed networks (primarily the frontoparietal and ventral attention networks). More goal-directed comprehension requires increased use of control/attention networks to facilitate a perceiver's comprehension goals. These findings identified the core network and the nature of its cooperation with control/attention networks during discourse comprehension. Thus, our findings could help refine and develop neurocognitive theories of discourse comprehension.

4.4. The functional significance of the default network

A topic of recent interest in the neurosciences concerns the function of the default network. Some studies have suggested a role of the default network in memory-based mental processing, such as semantic concept processing (Binder et al., 2009) and construction of episodic memory (Hassabis and Maguire, 2007). Other studies have noted the involvement of the default network in social-cognition tasks, such as theory of mind (Spreng and Grady, 2010) and affective processing (Amft et al., 2015). However, while these cognitive processes appear quite diverse, they likely are all related to processing of the self and others; namely, social tasks. Thus, a central question has emerged as to whether the core function of the default network is social-cognitive processing (Spreng and Andrews-Hanna, 2015).

In the present study, we showed that discourse comprehension recruited the default network to a large extent. This pattern was found both in the overall analysis and for all sub-processes. Of the sub-processes considered, pragmatic interpretation has been most frequently related to social cognition (e.g., Bambini et al., 2011; Diaz and Hogstrom, 2011; Eviatar & Just, 2006). A larger proportion of activations was found in the default network for pragmatic interpretation (91.1%), which could indicate that this network is sensitive to social cognitive processing. However, even without apparent social processing, the default network was substantially recruited during discourse processing, especially for consistent text integration (88.4%) in which social content was often well-matched between analysis contrasts. These findings could indicate that the default network not only supports the processing of social information, but also subserves the mental construction of a more generalized set of information. These observations compare favorably with one of our previous studies (Lin et al., 2018). In that study, we observed that the theory of mind network, which involves similar brain regions to the discourse comprehension network, could be decomposed into regions supporting domain-specific integration of social semantic content and also regions supporting domain-general semantic integration.

Note that the default network is typically observed during resting state when participants do nothing while inside the scanner. However, doing "nothing" involves a lot of mind wondering, inner speech, and mental model construction which are all related to discourse construction. In Jacobs and Willems (2018), the authors have argued that rest can be regarded as an active state of situation model construction with poorly defined instructions. Accordingly, one should not be surprised that the default network that is typically found during rest also activates during discourse comprehension (Jacobs and Willems, 2018). In light of these views, perhaps a better perspective to think of the function of default network would be that discourse processing is at the core of doing "nothing" which is the process that activates the default network.

Regarding the mechanism by which the default network processes information, previous studies have argued for segregation of the default network into three subsystems (the core, and temporal medial and dorsal medial subsystems) that respond to different processing demands. Several studies have proposed that constructing a mental representation based on memory is supported by the temporal medial subsystem (Andrews-Hanna et al., 2010; Christoff et al., 2016). However, others have argued that the temporal medial subsystem only provides information from prior experiences that are the building blocks of mental simulation and that the dorsal medial subsystem uses these building blocks to form mental representations (Buckner, et al., 2008).

Probing the function of the default network and its subsystems, we found that, of the three subsystems, the dorsal medial subsystem was most heavily weighted during discourse comprehension. A very small portion of the temporal medial subsystem was observed to be active during discourse comprehension. Thus, while the temporal medial subsystem is often related to memory construction (Andrews-Hanna et al., 2010; Christoff et al., 2016), it does not seem to be involved in discourse comprehension. One possible explanation for this is that the temporal medial subsystem primarily supports mental construction based on

episodic memory, while discourse comprehension is largely based on discourse content, but not episodic memory. The heavy weighting of the dorsal medial subsystem during discourse comprehension indicates that the construction of discourse representations is primarily realized by the dorsal medial subsystem. This could help clarify the functions of the subsystems within the default network.

5. Conclusions

Discourse processing involves a widely distributed neural system. Here, we demonstrated that the brain regions within this system are grouped into sub-systems, each supporting different sub-processes of discourse comprehension. We also found that the left inferior frontal gyrus and middle temporal gyrus serve as core regions across all sub-processes. At the large-scale network level, we provided direct evidence that the default network, particularly its dorsal medial subsystem, is the core network underlying discourse comprehension. Moreover, we revealed how different large-scale networks cooperate in discourse comprehension and its sub-processes. These findings extend current knowledge of functional subdivisions within the neural system underlying discourse comprehension and newly illuminate how brain regions work at large-scale network levels during discourse comprehension.

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