

# Neural mechanisms of discourse comprehension: a human lesion study

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Discourse comprehension is a hallmark of human social behaviour and refers to the act of interpreting a written or spoken message by constructing mental representations that integrate incoming language with prior knowledge and experience. Here, we report a human lesion study ( $n = 145$ ) that investigates the neural mechanisms underlying discourse comprehension (measured by the Discourse Comprehension Test) and systematically examine its relation to a broad range of psychological factors, including psychometric intelligence (measured by the Wechsler Adult Intelligence Scale), emotional intelligence (measured by the Mayer, Salovey, Caruso Emotional Intelligence Test), and personality traits (measured by the Neuroticism-Extraversion-Openness Personality Inventory). Scores obtained from these factors were submitted to voxel-based lesion-symptom mapping to elucidate their neural substrates. Stepwise regression analyses revealed that working memory and extraversion reliably predict individual differences in discourse comprehension: higher working memory scores and lower extraversion levels predict better discourse comprehension performance. Lesion mapping results indicated that these convergent variables depend on a shared network of frontal and parietal regions, including white matter association tracts that bind these areas into a coordinated system. The observed findings motivate an integrative framework for understanding the neural foundations of discourse comprehension, suggesting that core elements of discourse processing emerge from a distributed network of brain regions that support specific competencies for executive and social function.

**Keywords:** discourse comprehension; psychometric intelligence; emotional intelligence; personality traits; voxel-based lesion-symptom mapping

**Abbreviation:** WAIS-III = Wechsler Adult Intelligence Scale, third edition

## Introduction

Discourse comprehension is the act of interpreting a written or spoken message by constructing mental representations that integrate incoming language with prior knowledge and experience. To illustrate, consider the proposition, 'Michelle ordered a drink at the bar'. The meaning of the verb 'ordered' entails that she carried out a series of actions that resulted in a drink being delivered. The fact that we tend to interpret the sentence as ordering an alcoholic drink illustrates the role of background knowledge. Thus, discourse comprehension depends on understanding syntactic expressions (e.g. the meaning of the verb 'to order') that additionally incorporate background knowledge and experience to support a coherent understanding of the discourse as a whole (e.g. that Michelle is likely to order a specific type of drink and to be at a particular location, on a specific occasion, with specific people, etc.).

According to an influential theory of discourse processing (Dijk and Kintsch, 1983; Zwaan and Radvansky, 1998), understanding discourse depends on a mental model of what the written or spoken message says (the text base), in addition to a mental representation of what the message is about (the situation model). The propositional structure of the message is represented by the written or spoken sentence(s) and is supplemented by inferences that make the meaning of the sentence(s) locally coherent (e.g. by integrating multiple propositional elements of a complex message). The situation model is formed from the text base by combining background knowledge and experience to support a specific spatial, temporal, and/or psychological vantage point from which we perceive and understand the event(s). According to this framework, mental representations of the text base primarily depend on language processes that capture the propositional structure of the written or spoken message. In contrast, a situation model depends on executive functions for the integration of non-propositional and non-verbal information that represents the spatial, temporal, and/or psychological context for understanding the event(s). Contemporary research and theory on discourse comprehension investigates the nature of these representations, their neurobiological foundations, and how these representations unfold during online comprehension to support goal-directed social behaviour (Stemmer and Whitaker, 2008).

Neuroscience evidence indicates that a distributed network of cortical regions supports mental representations of word-level processes for understanding what a written or spoken message says (the text base). This network entails classic perisylvian language areas within the middle and superior temporal gyri and inferior frontal cortex (Robertson *et al.*, 1988; Huettner *et al.*, 1989; Binder *et al.*, 1994; Fletcher *et al.*, 1995; Fiez and Petersen, 1998; Maguire *et al.*, 1999; St George *et al.*, 1999; Giraud *et al.*, 2000; Ferstl and von Cramon, 2001, 2002; Vogeley *et al.*, 2001; Turkeltaub *et al.*, 2002; Ferstl *et al.*, 2005; Xu *et al.*, 2005; Vigneau *et al.*, 2006; Hasson *et al.*, 2007). Recent neuroscience evidence further indicates that specific cortical regions are preferentially engaged during the comprehension of coherent and connected texts, beyond comprehension of word-level representations. The observed cortical regions include the anterior temporal lobes (Stowe *et al.*, 1998; Ferstl *et al.*, 2008)

and orbitofrontal cortex (Xu *et al.*, 2005; Hasson *et al.*, 2007; Egidi and Caramazza, 2013), which are each high-level association cortices that integrate information across multiple brain systems and are believed to play an important role in the neural representation of situation models.

Accumulating neuroscience evidence further indicates that inferential processes for building coherent mental models that integrate incoming language with prior knowledge and experience depend on a distributed network of frontal and parietal brain regions (Badre and Wagner, 2006; Glascher *et al.*, 2010; Barbey *et al.*, 2012b). The fronto-parietal network includes lateral frontopolar cortex, anterior prefrontal cortex, dorsolateral prefrontal cortex, anterior cingulate/medial prefrontal cortex, and the inferior and superior parietal lobe. This constellation of regions is commonly engaged by tasks that require executive control processes (Ramnani and Owen, 2004). The fronto-parietal network is recruited by paradigms that elicit controlled processing related to the simultaneous consideration of multiple interdependent contingencies (Kroger *et al.*, 2002), conflicting stimulus-response mappings (Crone *et al.*, 2006), and integrating working memory with attentional resource allocation (Koechlin *et al.*, 1999). In addition, many of the regions in the fronto-parietal network show sustained activity over the duration of a task block (Dosenbach *et al.*, 2006), supporting the maintenance and integration of items for goal-directed behaviour. Thus, emerging evidence indicates that discourse comprehension may depend on a fronto-parietal network that supports the integration and control of cognitive representations and provides a neural architecture for building coherent mental models that integrate incoming language with prior knowledge and experience (Botvinick *et al.*, 2001; Miller and Cohen, 2001; Duncan, 2010).

The neuroscience literature on discourse comprehension is characterized by additional questions that remain the focus of ongoing research and scientific exchange. First, the degree to which discourse comprehension preferentially engages brain mechanisms within the left versus right hemisphere remains unclear. For example, investigators have proposed that general cognitive mechanisms for attention, memory, and executive processes within the left hemisphere are critical for discourse comprehension (Maguire *et al.*, 1999). Alternatively, research suggests that a core facet of discourse comprehension is the interpretation of non-literal meanings and that discourse comprehension may therefore engage a right lateralized brain network that supports inductive inference (Winner *et al.*, 1998; Brownell and Stringfellow, 1999; Beeman *et al.*, 2000; Robertson *et al.*, 2000). Second, it is unclear whether discourse comprehension depends on narrative-specific neural systems or a broader set of neural mechanisms for social information processing (Glascher *et al.*, 2010; Barbey *et al.*, 2012b; Barbey *et al.*, 2012a). A network of neural correlates has been linked to social and emotional processing using a range of experimental materials such as interpersonal scenarios, cartoons, jokes, sarcasm, faux pas, and moral and ethical dilemmas (Adolphs, 2010). Analysis of the specialized contributions of regions within the social knowledge network has suggested, for example, that the orbitofrontal cortex plays a key role in the representation of mental states, both for an individual's own thoughts and beliefs and those of others, and the left anterior temporal lobe

is involved in storing relevant social knowledge, which contributes to the contextual understanding of others' social interactions (Frith and Frith, 2003; Sabbagh, 2004; Saxe, 2006). Thus, the observed network engages regions implicated in discourse comprehension and may reflect key competencies for social information processing. In addition, research on discourse comprehension in cognitive ageing indicates that decline in semantic integration in comprehension of written texts is associated with recall abilities (measured by reading span) and emotional regulation (Maguire *et al.*, 1999; Smiler *et al.*, 2003; Egidi and Nusbaum, 2012; Payne *et al.*, 2012), further suggesting a dependency between discourse comprehension and executive, social and emotional processes. Finally, the contribution of mechanisms for learning and memory to discourse comprehension remains to be well characterized. Behaviourally, the use of situation models aids comprehension and memory of discourse considerably (Gernsbacher, 1990) and an emerging body of neuroscience evidence further suggests that discourse comprehension and production abilities may critically depend on executive and attentional processes within the prefrontal cortex (Alexander, 2006; Ferstl *et al.*, 2008).

Research on the neural bases of discourse comprehension would therefore benefit from a more precise characterization of its cognitive foundations, applying a psychometric approach to identify key competencies of discourse comprehension and their relation to a broad spectrum of psychological factors. The application of lesion methods to map the information processing architecture of discourse comprehension would further advance our understanding of the mechanisms that give rise to discourse processing (Glascher *et al.*, 2010; Woolgar *et al.*, 2010; Barbey *et al.*, 2012b). Neuropsychological patients with focal brain lesions provide a valuable opportunity to study the neural mechanisms of discourse processing, supporting the investigation of lesion-deficit associations that elucidate the role(s) of specific brain structures. Accumulating evidence suggests, for example, that social-communicative deficits after brain injury may result from damage to the prefrontal cortex and deficits in the ability to represent situation models that guide the selection and control of responses to social stimuli (Barbey *et al.*, 2009a; Barbey *et al.*, 2009b; Adolphs, 2010; Barbey, 2011a; Barbey *et al.*, 2013a, in press). Although the neural foundations of discourse processing remain to be assessed using lesion mapping methods, the broader neuropsychological patient literature has provided significant insight into the neural bases of higher cognitive functions, such as general intelligence (Basso *et al.*, 1973; Black, 1976; Eslinger and Damasio, 1985; Shallice and Burgess, 1991; Bechara *et al.*, 1994; Duncan *et al.*, 1995; Burgess and Shallice, 1996; Isingrini and Vazou, 1997; Parkin and Java, 1999; Blair and Cipolotti, 2000; Kane and Engle, 2002; Bugg *et al.*, 2006; Glascher *et al.*, 2009, 2010; Roca *et al.*, 2010; Barbey *et al.*, 2012b) and working memory (D'Esposito and Postle, 1999; Muller *et al.*, 2002; Baldo and Dronkers, 2006; D'Esposito *et al.*, 2006; Volle *et al.*, 2008; Tsuchida and Fellows, 2009). These studies, however, share one or more of the following features: diffuse (rather than focal) brain lesions, lack of comparison subjects carefully matched for pre- and post-injury performance measures, exclusive use of cognitive tests without an assessment of discourse comprehension, and lack of latent variable modelling to derive error-free indices of the

psychological constructs of interest. As a consequence, there has been no comprehensive evaluation of discourse comprehension in a relatively large sample of patients with focal brain damage, and across a broad range of tasks and stimulus material.

Motivated by these considerations, the cognitive and neural bases of discourse comprehension were studied here in a large sample of patients with focal brain injuries ( $n = 145$ ). Discourse comprehension was analysed in relation to a broad set of psychological factors, including psychometric intelligence (Wechsler Adult Intelligence Scale), emotional intelligence (Mayer, Salovey, Caruso Emotional Intelligence Test), and personality traits (Neuroticism-Extroversion-Openness Personality Inventory). Finally, voxel-based lesion-symptom mapping was applied to elucidate the underlying information processing architecture, identifying core brain mechanisms that support discourse comprehension.

## Materials and methods

### Participant data

Participants were drawn from the Phase 3 Vietnam Head Injury Study (VHIS) registry, which includes American male veterans who suffered brain damage from penetrating head injuries in the Vietnam War ( $n = 145$ ). All subjects gave informed written consent. Phase 3 testing occurred between April 2003 and November 2006. Demographic and background data for the VHIS are reported in Supplementary Table 1 (Koenigs *et al.*, 2009; Raymont *et al.*, 2010; Barbey *et al.*, 2011b, 2012b). No effects on test performance were observed in the VHIS sample on the basis of demographic variables (e.g. age, years of education, lesion size).

### Lesion analysis

CT data were acquired during the Phase 3 testing period. Axial CT scans without contrast were acquired at Bethesda Naval Hospital on a GE Medical Systems Light Speed Plus CT scanner in helical mode (150 slices per subject, field of view covering head only). Images were reconstructed with an in-plane voxel size of  $0.4 \times 0.4$  mm, overlapping slice thickness of 2.5 mm, and a 1 mm slice interval. Lesion location and volume were determined from CT images using the Analysis of Brain Lesion software (Makale *et al.*, 2002; Solomon *et al.*, 2007) contained in MEDx v3.44 (Medical Numerics) with enhancements to support the Automated Anatomical Labeling atlas (Tzourio-Mazoyer *et al.*, 2002). Lesion volume was calculated by manual tracing of the lesion in all relevant slices of the CT image then summing the traced areas and multiplying by slice thickness. Lesion tracing included grey and white matter regions damaged as a consequence of penetrating head injury (e.g. incorporating coup–contrecoup effects and axonal injury). We note that the effects of penetrating head injuries are more focal and less susceptible to diffuse axonal injury than typical blunt head injuries. A trained neurologist performed the manual tracing, which was then reviewed by an observer who was blind to the results of the neuropsychological testing. As part of this process, the CT image of each subject's brain was spatially normalized to a CT template brain image. This template was created by spatial normalization of a neurologically healthy individual's CT brain scan to MNI space (Collins *et al.*, 1994) using the Automated Image Registration program (Woods *et al.*, 1993). For each subject, a lesion mask image in MNI space was saved for voxel-based lesion-symptom mapping



(Bates *et al.*, 2003). This method applies a Mann-Whitney U-test to compare, for each voxel, scores from patients with a lesion at that voxel contrasted against those without a lesion at that voxel. The reported findings were thresholded using a False Discovery Rate correction of  $q < 0.01$ . To ensure sufficient statistical power for detecting a lesion-deficit correlation, our analysis only included voxels for which three or more patients had a lesion. The lesion overlap map for the entire VHIS patient sample is illustrated in [Supplementary Fig. 1](#).

## Psychological measures

We administered the Discourse Comprehension Test, which is designed to provide information about language comprehension as it occurs in natural communicative interactions (Brookshire and Nicholas, 1984; Wegner *et al.*, 1984; Nicholas and Brookshire, 1986). The Discourse Comprehension Test assesses comprehension and retention of stated and implied main ideas and details from 10 stories with questions that require yes/no responses. 'Main ideas' represent what is most relevant or important (i.e. the gist) and provide an overall unity to discourse. In contrast, 'details' represent specific elements of discourse that may be peripheral to the main ideas. Whereas main ideas are expressed by phrases or sentences, details are typically encoded by individual elements of discourse (e.g. nouns, verbs, etc.). Finally, the directness of main ideas and details may be stated 'explicitly' or 'implied' in the text. The stories of the Discourse Comprehension Test are controlled for length, grammatical complexity, listening difficulty and information content. In addition, we administered the Wechsler adult intelligence scale, third edition (WAIS-III; Wechsler, 1997), the Mayer, Salovey, Caruso Emotional Intelligence Test (MSCEIT; Mayer *et al.*, 2008), and the Neuroticism-Extraversion-Openness Personality Inventory (NEO-PI; Costa and McCrae, 2000).

We obtained latent variables representative of psychometric and emotional intelligence as reported by Barbey *et al.* (2012b). Latent factors for psychometric intelligence were derived from the WAIS-III, namely, verbal comprehension/crystallized intelligence (vocabulary, similarities, information, and comprehension), perceptual organization/fluid intelligence (block design, matrix reasoning, picture completion, picture arrangement, and object assembly), working memory capacity (arithmetic, digit span, and letter-number sequencing), and processing speed (digit symbol coding and symbol search). The MSCEIT allowed the extraction of a general emotional intelligence index (faces, pictures, sensations, facilitation, blends, changes, emotional, and social subtests). Personality traits were measured by the NEO-PI, but treated separately from the cognitive measures. Discourse comprehension scores were obtained directly from the Discourse Comprehension Test (stated/implied main ideas, stated/implied details). [Supplementary Table 2](#) summarizes the employed measures of psychometric and emotional intelligence (for further detail concerning their standardization, reliability, and validity, see Wechsler, 1997; Mayer *et al.*, 2008). [Supplementary Table 3](#) provides descriptive statistics for each of the administered neuropsychological tests.

## Voxel-based lesion-symptom mapping

The obtained scores were correlated to regional grey and white matter determined by voxel-based lesion-symptom mapping (Bates *et al.*, 2003). This method compares, for every voxel, scores from patients with a lesion at that voxel contrasted against those without a lesion at that voxel. This approach can help to identify brain regions that are important for the constructs of interest by mapping where damage can interfere with performance (Glascher

*et al.*, 2010; Woolgar *et al.*, 2010; Barbey *et al.*, 2012b; Barbey *et al.*, 2012a; Barbey *et al.*, in press).

# Results

## Behavioural results

[Table 1](#) reports the correlation matrix for the 12 measures of interest. Note that discourse comprehension performance showed significant correlations with all the psychometric and emotional intelligence scores (from  $r = 0.28$  to  $r = 0.36$ ). Extraversion was the personality trait more highly correlated with discourse comprehension ( $r = -0.15$ ). These are moderate correlations, meaning that there is substantial variance left in discourse comprehension performance. Therefore, we computed stepwise regression analyses for obtaining residual discourse comprehension scores orthogonal to its significant predictors, as explained below.

## Stepwise regression

Psychometric intelligence factors (verbal comprehension, fluid intelligence, working memory, and processing speed) and emotional intelligence, along with personality traits were submitted to a stepwise regression analysis; discourse comprehension was the dependent measure. The results showed that working memory and extraversion reliably predict discourse comprehension. Standardized beta values were: working memory ( $\beta = 0.37$ ,  $P = 0.000$ ) and extraversion ( $\beta = -0.16$ ,  $P = 0.04$ ). Therefore, higher working memory scores and lower extraversion scores predict better discourse comprehension performance. The variance unexplained by working memory and extraversion defined a residual discourse comprehension score that was also submitted to lesion analysis.

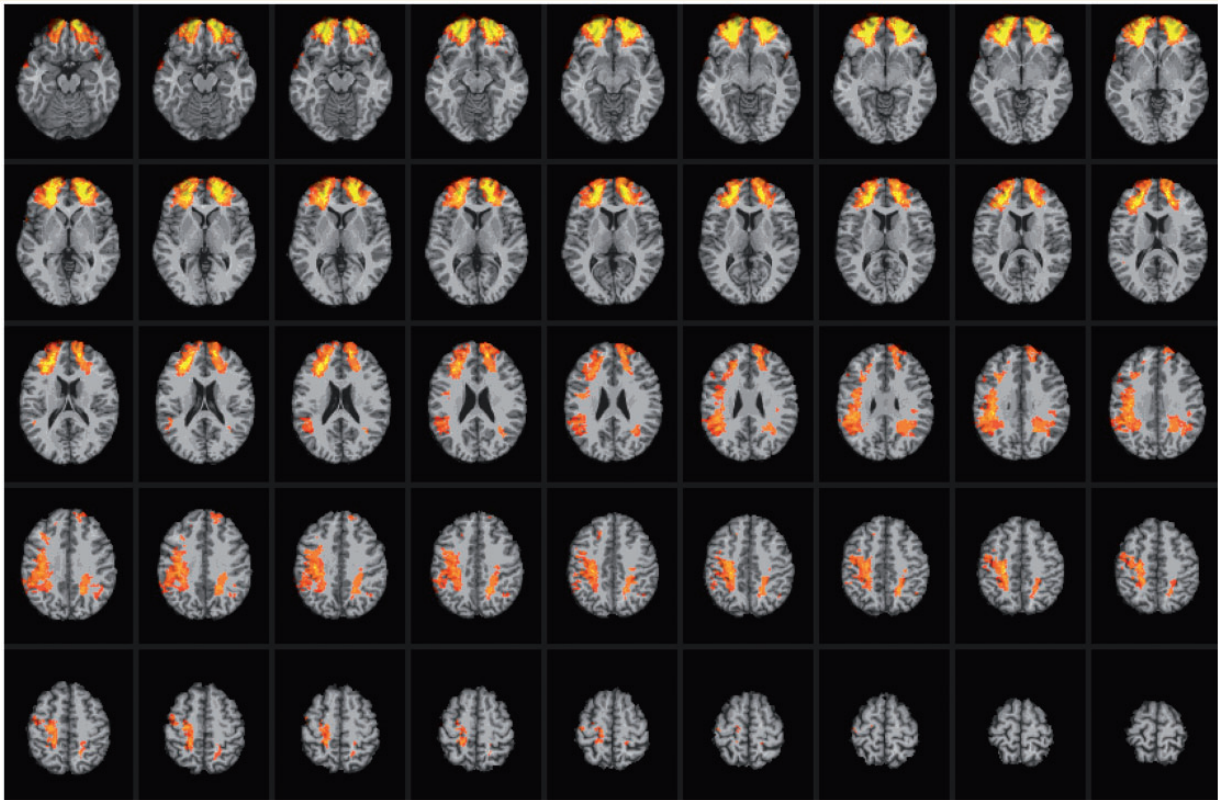
## Discourse comprehension: lesion results

Discourse comprehension was associated with a distributed network of brain regions within the left and right hemisphere ([Fig. 1](#)). Significant effects encompassed locations for: (i) language processing (e.g. Broca's area and superior temporal gyrus); (ii) spatial processing (e.g. inferior and superior parietal cortex); (iii) motor processing (e.g. somatosensory and primary motor cortex); and (iv) working memory (e.g. dorsolateral prefrontal cortex, inferior and superior parietal cortex, and superior temporal gyrus); in addition to expected locations of major white matter fibre tracts, including (v) the anterior and dorsal bundle of the superior longitudinal/arcuate fasciculus connecting temporal, parietal, and inferior frontal regions; (vi) the superior fronto-occipital fasciculus connecting dorsolateral prefrontal cortex and the frontal pole with the superior parietal lobule; and (vii) the uncinate fasciculus, which connects anterior temporal cortex and amygdala with orbitofrontal and frontopolar regions. This pattern of findings suggests that discourse comprehension reflects the ability to integrate verbal, spatial, motor, and executive processes through a circumscribed set of cortical connections within the left and right hemisphere.

**Table 1** Correlation matrix for all scores ( $n = 145$ ),  $P$ -values are shown

	1	2	3	4	5	6	7	8	9	10	11	12
1. Latent WAIS Verbal Comprehension		0.585	0.755	0.446	0.809	−0.071	0.107	−0.007	−0.083	0.308	0.322	0.039
2. Latent WAIS Perceptual Organization	0.000		0.000	0.000	0.000	0.398	0.200	0.933	0.320	0.000	0.000	0.644
3. Latent WAIS Working Memory		0.646		0.794	0.550	−0.042	0.147	0.005	−0.069	0.177	0.283	0.070
4. Latent WAIS Processing Speed		0.000	0.000		0.000	0.615	0.079	0.951	0.413	0.033	0.001	0.405
5. Latent Emotional Intelligence			0.602	0.607		0.035	0.114	−0.023	−0.128	0.186	0.364	0.076
6. NEO: Extraversion			0.000	0.000		0.676	0.172	0.786	0.125	0.025	0.000	0.365
7. NEO: Agreeableness				0.498		0.039	−0.001	0.020	−0.070	0.097	0.284	0.089
8. NEO: Conscientiousness				0.000		0.642	0.993	0.812	0.403	0.245	0.001	0.288
9. NEO: Neuroticism						−0.060	0.133	0.193	−0.078	0.273	0.333	0.041
10. NEO: Openness						0.476	0.110	0.020	0.352	0.001	0.000	0.624
11. Discourse Comprehension: Overall Score							0.129	−0.001	−0.246	0.163	−0.148	−0.156
12. Discourse Comprehension Residual							0.122	0.994	0.003	0.050	0.075	0.062
								−0.068	−0.239	0.122	0.079	0.037
								0.419	0.004	0.142	0.343	0.660
									0.059	0.018	0.002	−0.031
									0.480	0.831	0.977	0.709
										−0.064	−0.136	−0.106
										0.442	0.103	−0.106
											0.016	−0.074
											0.847	0.378
												0.945
												0.000

NEO = Neuroticism-Extraversion-Openness.



**Figure 1** Voxel-based lesion-symptom mapping of discourse comprehension ( $n = 145$ ). The illustrated results are thresholded at  $q < 0.01$  (using a false discovery rate correction for multiple comparisons). In each axial slice, the right hemisphere is to the left.

## Working memory: lesion results

As illustrated in Fig. 2, discourse comprehension shared neural substrates with working memory, engaging left inferior [Brodmann area (BA) 7] and superior parietal regions (BA 40), and right dorsolateral prefrontal cortex (BA 9) (Fig. 2). These frontal and parietal regions have been widely implicated in the maintenance, monitoring and manipulation of representations in working memory (Wager and Smith, 2003; Owen *et al.*, 2005) and provide evidence in this context for their central roles in discourse comprehension.

## Residual discourse comprehension scores: lesion results

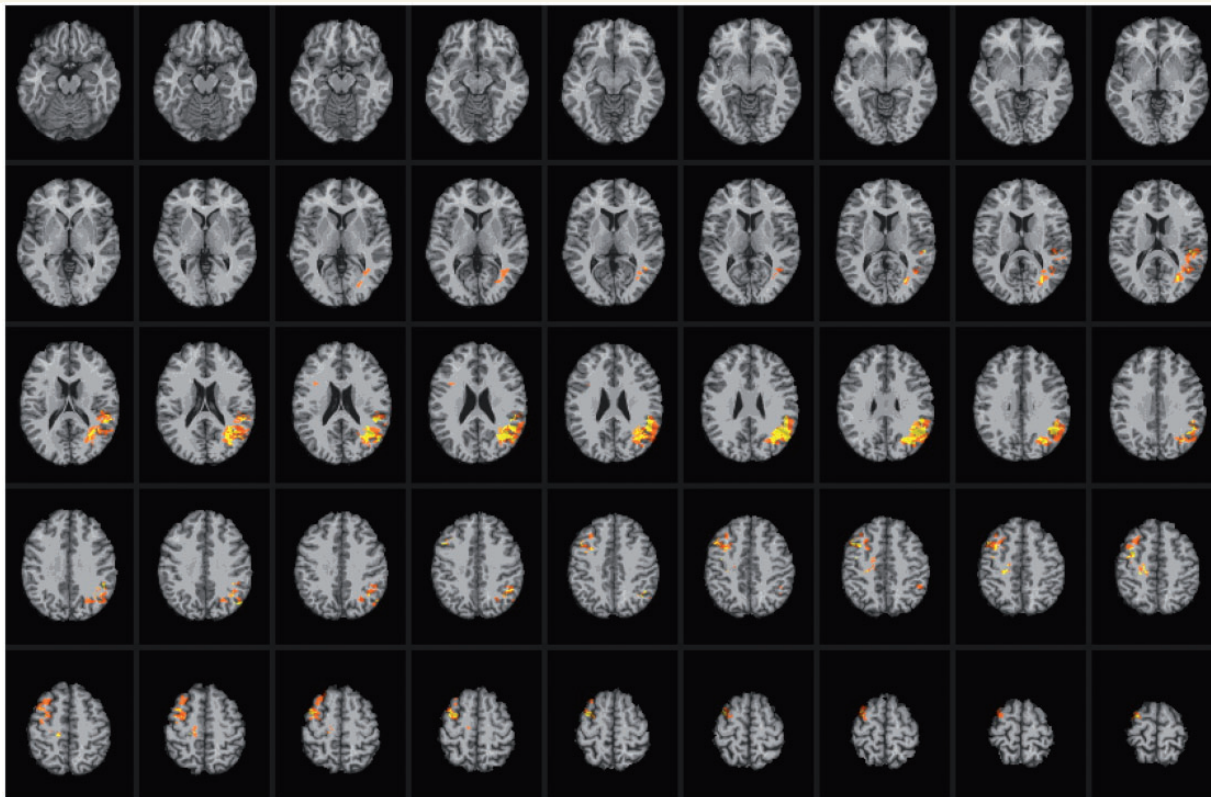
We analysed the discourse comprehension residual scores removing variance shared with its significant predictors. As Table 1 illustrates, the discourse comprehension residual scores were not reliably correlated with any of the psychometric, emotional, or personality variables examined in the present study (e.g. verbal comprehension, perceptual organization, working memory, etc.). This residual factor captures the unique variance associated with discourse comprehension and supports an assessment of the core brain mechanisms underlying discourse processes. Similar findings for the discourse comprehension latent and residual scores are expected due to the large correlation between these factors ( $r = 0.94$ ,  $P = 0.000$ ). Impairment in the discourse comprehension

residual score was associated with selective damage to frontal and parietal brain structures that have been widely implicated in executive (Miller and Cohen, 2001) and social function (Ochsner and Lieberman, 2001; Ochsner, 2004). These regions comprised bilateral orbitofrontal cortex (BA 10), bilateral inferior (BA 40) and superior parietal cortex (BA 7), in addition to major white matter fibre tracts, including the superior longitudinal/arcuate fasciculus and the superior fronto-occipital fasciculus (Fig. 3). The observed pattern of findings indicates that discourse comprehension is centrally supported by executive, social, and emotional processes (Ochsner and Lieberman, 2001; Ochsner, 2004).

## Discussion

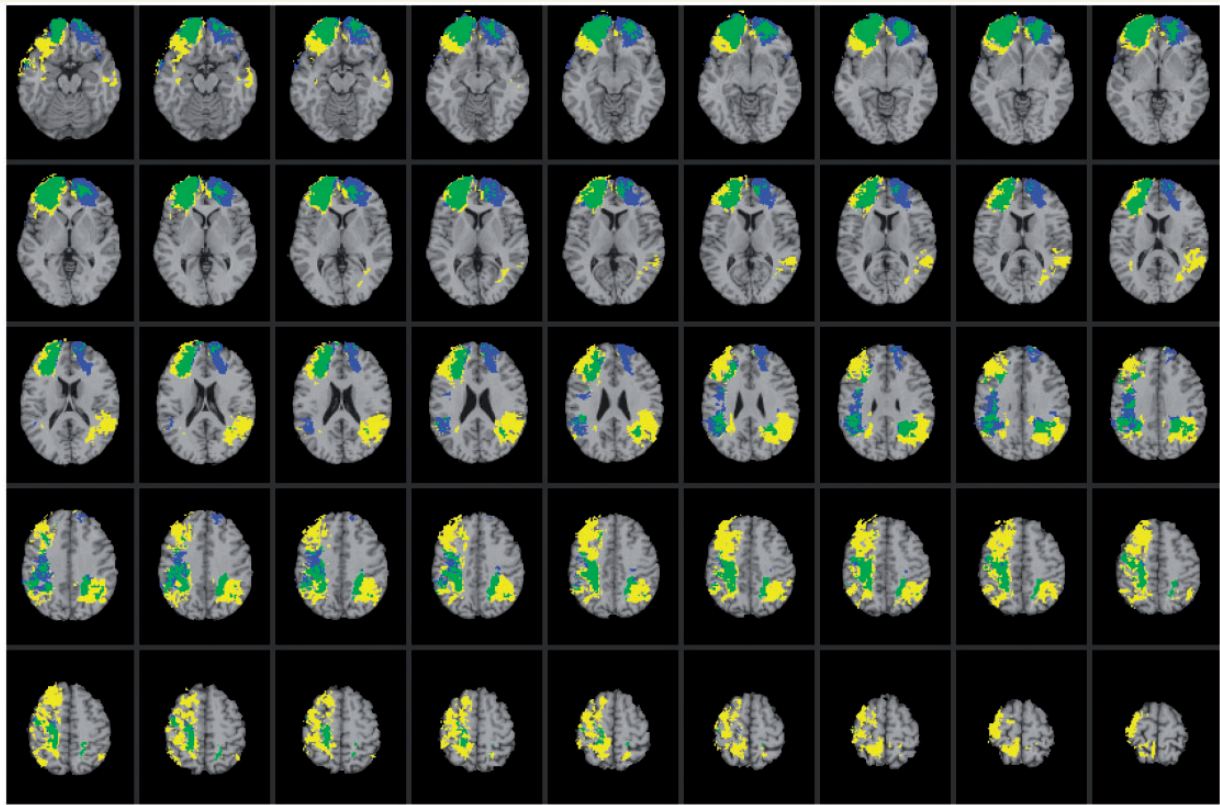
We investigated the neural bases of discourse comprehension and systematically examined their contributions to a broad set of psychological factors, including psychometric intelligence, emotional intelligence, and personality traits. Using a relatively large sample of patients with focal brain injuries ( $n = 145$ ), we report several main findings.

First, raw correlations among psychometric intelligence (verbal comprehension/crystallized intelligence, perceptual organization/fluid intelligence, working memory, and processing speed), emotional intelligence, personality traits, and discourse comprehension showed that (i) psychometric and emotional intelligence scores were positively correlated with discourse comprehension; and



**Figure 2** Voxel-based lesion-symptom mapping of working memory ( $n = 145$ ). The illustrated results are thresholded at  $q < 0.01$  (using a false discovery rate correction for multiple comparisons). In each axial slice, the right hemisphere is to the left.





**Figure 3** Voxel-based lesion-symptom mapping of discourse comprehension and discourse comprehension (residual) ( $n = 145$ ). Lesion overlap map illustrating common and distinctive brain regions for discourse comprehension (blue) and discourse comprehension residual (yellow) ( $n = 145$ ;  $q < 0.01$ ). Overlap between these factors is illustrated in green. In each axial slice, the right hemisphere is to the left.

(ii) extraversion was negatively correlated with discourse comprehension. Therefore, discourse comprehension depends on psychometric and emotional intelligence factors and the regulation of social information processing (reduction in impulsivity and inappropriate social behaviour associated with high levels of extraversion).

Second, stepwise regression analyses showed that working memory capacity and extraversion reliably predict discourse comprehension performance. This result indicates that verbal comprehension, perceptual organization, processing speed, and emotional intelligence are no longer related to discourse comprehension. The regression analysis also demonstrated that there is a substantial proportion of discourse comprehension variance that is unexplained by the considered predictors.

Third, voxel-based lesion-symptom mapping of discourse comprehension and its reliable predictors revealed that these convergent variables engage a shared network of frontal and parietal regions. The observed findings contribute to the neuropsychological patient evidence indicating that damage to a distributed network of frontal and parietal regions is associated with impaired performance on tests of executive processing (Jung and Haier, 2007; Chiang *et al.*, 2009; Colom *et al.*, 2009; Glascher *et al.*, 2010; Barbey *et al.*, 2012a; Barbey and Patterson, 2011; 2013b) and social function (Barbey *et al.*, 2012a). Barbey *et al.* (2012a) applied voxel-based lesion-symptom mapping to elucidate the

neural substrates of psychometric  $g$ , reporting a left lateralized fronto-parietal network that converges with the pattern of findings observed here. The present study contributes to this research programme by elucidating the relationship between key competencies of intelligence and discourse comprehension, providing evidence that these domains recruit a highly overlapping and broadly distributed network of frontal and parietal regions (Figs 1–3). We further investigated the neural basis of discourse comprehension while removing the variance shared with its significant predictors. This analysis revealed selective damage to frontal and parietal brain structures that have been widely implicated in executive processes (Miller and Cohen, 2001) and social function (Ochsner and Lieberman, 2001; Ochsner, 2004) (Fig. 3).

Accumulating evidence indicates that the fronto-parietal network provides a coordinated architecture for the integration and control of cognitive representations (Glascher *et al.*, 2010; Barbey *et al.*, 2012b). Our findings suggest that mechanisms for integration and control are critical for discourse comprehension—supporting the construction of coherent mental models that integrate incoming language with prior knowledge and experience. In particular, the results indicate that discourse comprehension depends on mental representations that integrate verbal, spatial, motor, and executive processes through a circumscribed set of cortical connections within the left and right hemisphere (Fig. 1). This finding supports theories of discourse comprehension that posit

general cognitive mechanisms within the left hemisphere (Maguire *et al.*, 1999) and processes for the interpretation of non-literal meanings within the right hemisphere (Winner *et al.*, 1998; Brownell and Stringfellow, 1999; Beeman *et al.*, 2000; Robertson *et al.*, 2000). Taken together, these results support a multifaceted theory of discourse comprehension that incorporates psychological mechanisms for executive function (i.e. integration and control of cognitive representations, and working memory capacity) and normative social behaviour (i.e. negative correlation with impulsivity and inappropriate social behaviour). Rather than operating on the basis of distinct mechanisms, discourse comprehension appears to share cognitive and neural mechanisms with systems for working memory and social information processing (Figs 1–3).

This conclusion complements emerging psychological research that examines discourse comprehension beyond traditionally studied reader and text variables. The focus of recent investigations includes executive functions (Stoltzfus *et al.*, 1993; Kane *et al.*, 1994; Chiappe *et al.*, 2000), such as the readers' propensity to monitor their understanding (Theide, 2010), and their reliance upon credible and non-credible information sources (Sparks and Rapp, 2011), in addition to social and emotional factors, such as affective influences on comprehension (Komeda, 2009). A growing number of researchers have suggested that theories of discourse comprehension must account for these types of processes, which constitute our naturalistic comprehension experiences (Gerrig, 1993). Indeed, the observed human lesion results suggest that discourse comprehension depends on mechanisms for executive and social function and provide a cognitive neuroscience framework for understanding naturalistic comprehension experiences.

Finally, it is important to emphasize that the abilities measured by tests of psychometric intelligence, emotional intelligence, and personality do not provide a comprehensive assessment of all human psychological traits. There are other aspects, in addition to those measured here, which may contribute to discourse comprehension. For example, investigating how readers interact with and build meaning from multiple related texts remains an important issue (Goldman, 2004). Consider that the Internet affords individuals the opportunity to read multiple, conflicting accounts of current events (Rouet, 2006), or that history students must integrate across multiple texts to understand a historical incident (Wineburg, 2001). Explaining such everyday experiences requires closer examination of multiple texts and their implications for executive control and working memory (Barbey *et al.*, 2013b, 2013c). Another important issue for discourse comprehension research involves investigating how individuals revise their prior beliefs during discourse comprehension, a process called 'memory updating', which has been strongly tied to working memory capacity (Colom, 2008; Martinez *et al.*, 2011). Research on memory updating has examined the types of texts, reader variables, and task instructions that make revision more likely. Readers often rely on information mentioned early in a text, even when that information is discounted or contradicted (Johnson, 1994; O'Brien, 2010). Memory updating is facilitated by texts that contain causal explanations for why outdated information is no longer valid (Barbey and Patterson, 2011; Patterson, 2012), or by instructions asking readers to track unfolding text

events (Rapp, 2005). Additional research is necessary to examine the types of arguments that effectively encourage belief revision, given particular academic settings and styles of reading. Finally, further research is needed to better characterize the specific cognitive processes that contribute to discourse comprehension given, for example, in the present case it is not possible to isolate the contribution of word- or sentence-level mechanisms and to address the role of specific executive control mechanisms (e.g. inhibitory control, for example, measured by the Stroop task; Stoltzfus *et al.*, 1993; Kane *et al.*, 1994; Chiappe *et al.*, 2000; Raz *et al.*, 2011; Diamond, 2013). Understanding the cognitive and neural architecture of discourse comprehension will ultimately require a comprehensive assessment that examines a broader scope of issues. The reported findings contribute to this emerging research programme, demonstrating that discourse comprehension emerges from a distributed network of brain regions that support specific competencies for executive and social function.

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## Supplementary material

Supplementary material is available at *Brain* online.

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