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# **The neural basis of semantic processing across comprehension contexts**

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## **Publications and Contributions**

The empirical chapters of this thesis have been published or submitted for publication. This section lists the relevant publication corresponding to each chapter as well as the author contributions according to the Contributor Roles Taxonomy.

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## Abstract

Current neurobiological models of semantic cognition have been predominately derived from studies of single-words or sentences which may provide an impoverished estimate of how semantic processing occurs in real-world contexts. Studies that make use of more ecologically valid stimuli such as natural language or narratives suggest that, counter to the hub-and-spoke framework in which the anterior temporal lobe (ATL) serves as a graded hub integrating information from proximal sensorimotor spokes, the semantic system displays voxel-wise category specialization tiled across a large, distributed network. A complicating factor in reconciling these seemingly conflicting claims is the over-reliance on concrete conceptual knowledge in describing the organization of the semantic system. A recent theoretical account argues that social knowledge, like other types of semantic knowledge, is processed within the ventrolateral ATL, but this claim has not been tested using naturalistic stimuli, which better sample abstract social knowledge, including pragmatic inference.

This thesis investigates the organization of the semantic system across multiple scales, from isolated words to multimodal narratives, and across multiple types of semantic conceptual knowledge, from concrete to abstract. Using comprehension of concrete words as a starting point, the first study describes a critical examination of specialization within the semantic system for taxonomic (*dog – bear*) and thematic (*dog – leash*) relations using intracranial EEG recordings from an array of depth electrodes within ATL, inferior parietal lobule (IPL), and two regions within the semantic control network, inferior frontal gyrus (IFG) and posterior middle temporal gyrus (pMTG). Moving across the context and conceptual scale to build upon this work, the second study investigated how the concrete and abstract lexical and semantic properties of single-words, akin to those that informed the hub-and-spoke model, are processed in a complex, complete narrative presented to participants during fMRI scanning. In doing so, this study enabled comparisons between prior studies of isolated words and naturalistic work, thus moving toward an integrated cross-scale account of semantic cognition. Using the same neuroimaging data, the third study extended this work to investigate how context contributes to the construction of meaning by studying how the semantic and social cognitive systems are engaged by social and pragmatic sentence-level content. This enabled a direct,

naturalistic test of the claim that social knowledge is housed within the semantic system. The fourth study investigated shared processing between social and semantic systems using fMRI data collected during movie-viewing, which captures the multimodal environment in which social knowledge is exchanged.

The results of these studies collectively demonstrate that the semantic and social systems are differentially engaged across the scales investigated here. Concrete conceptual relations engage one (or more) specialized hubs within the semantic system, whereas processing of naturalistic verbal and event content co-varies with activation in large brain networks. There is evidence of functional gradations within ATL that are differentially sensitive to the demands of narrative comprehension – the anterior superior temporal gyrus (i.e., dorsolateral subregion) and anterior fusiform (i.e., ventral subregion) appear to be particularly sensitive to the quantity and informativeness of external input whereas the anterior middle and inferior temporal gyri (i.e., ventrolateral subregion) appear to be engaged by internal, or endogenous, semantic processing during narrative comprehension. Engagement of this same ventrolateral subregion is observed in response to social word and sentence content, providing support for the claim that social processing is subsumed within the semantic system. Taken together, the results suggest an extension to the current neurobiological model of semantic cognition that accommodates comprehension contexts. The studies undertaken as part of this thesis build upon the existing concept-level frameworks towards a narrative-level framework of semantic cognition.

## **Lay Summary**

A critical goal in research on human cognition is to understand how our brains make sense of the world around us. Existing models of how verbal and non-verbal knowledge, or semantic memory, is processed in the brain are based on studying responses to single words or sentences. This approach might not fully represent how our brain processes meaning in everyday life. How this system functions in real-world situations is particularly important for social communication and behaviour. A recent theory proposes that social knowledge is processed in the semantic system, but this has not been fully tested with realistic stimuli that better capture social processing and subtle social cues, like understanding implied meanings in conversations.

To explore this, this thesis examined how our brain's semantic system works at different levels, from understanding single words to complex stories like audiobooks and movies. It also looks at how our brain handles different types of knowledge, from tangible objects to abstract ideas. The studies described in this thesis use brain imaging techniques to see how different brain regions are engaged during these tasks.

The first study uses recordings from electrodes placed inside the brain to examine how the brain processes different types of concrete word relationships. The second study uses brain scans (functional MRI) to see how the brain processes the meaning of words and concepts within a complete story. The third study looks at how social and pragmatic content in sentences within the same story are processed within the brain's semantic and social cognitive systems. The fourth study uses fMRI during movie-watching to understand how the brain processes semantic and social knowledge in a multimodal narrative.

The results from these studies show that current models of the semantic system underestimate the extent and function of the system across naturalistic contexts. For concrete concepts, there is evidence of two "hub" regions. For more natural and complex content, such as audiobooks and movies, there is evidence of subregions within the semantic system that support different aspects of narrative comprehension: (1) processing the rapid and almost constant input, (2) accessing the meaning of the individual words, and (3) reflecting on how the information relates

to the overall narrative. Social processing, including making social inferences, appears to be supported by one of these subregions, consistent with the theory that social information is processed within the semantic system. Overall, this thesis provides a model for how our brains understand meaning in stories and highlights the need for a more comprehensive model that considers naturalistic contexts.

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# **Chapter 1**

## **INTRODUCTION**

The semantic memory system stores the conceptual knowledge we acquire as we navigate life, encountering new objects, engaging in new experiences, and interacting with other people (McRae & Jones, 2013). We flexibly, and often effortlessly, access this verbal and non-verbal knowledge to communicate complex and nuanced ideas, understand the connections between the objects and events we encounter, comprehend detailed stories and conversations, and recognise and describe our own and others' behaviour. Semantic cognition is thus integral to everyday life. Despite this, much of what is known about the neural basis of semantic cognition is based on studies conducted in constrained settings that minimally incorporate context as it occurs in the real world. This thesis sought to remedy this by examining comprehension across contexts – from word pairs having different semantic relations to audiobooks and movies.

The following sections provide a description of the current neurobiological model of semantic cognition including opportunities for advancement that were pursued in the studies in this thesis. The relevant literature motivating each study is contained within each empirical chapter and is only broadly outlined here to provide general background information and to help situate the studies in relation to each other. An overview of the studies included in this thesis is provided at the end of this chapter.

## **1 Current Neural Model**

### **1.1 *Hub-and-spoke model***

A confluence of multiple streams of complementary research undertaken over the course of the last several decades has resulted in a converging neurocomputational model of semantic cognition. Cognitive accounts of the acquisition and organisation of semantic knowledge were informed by research on embodied cognition (Barsalou et al., 2003) and computational models (Rogers & McClelland, 2004). In these accounts, semantic representations arise from sensory-motor experiences and are grounded in these features of the environment, but no claims about the neural

instantiations of this process are made. The Wernicke-Meynert model, an early precursor to the contemporary model, proposed that conceptualizations could arise from widespread and interconnected brain areas storing modality-specific information that are reactivated when an object or concept is re-encountered (Eggert, 1977). Building upon this idea, the “convergence-divergence zone” theory emerged to describe a general neural framework that aligned with these accounts, providing a precursor to the current prevailing model. In this neural architecture, amodal zones, or association cortices, interface with sensorimotor neurons via bidirectional projections which provides an account of how representational feature information is both acquired and combined during subsequent retrieval (Damasio, 1989).

Strong neural evidence of the central role of the anterior temporal lobe (ATL) in semantic cognition emerged from neuropsychological research focusing on impaired semantic processing in semantic dementia, or semantic variant primary progressive aphasia, which results in neurodegeneration of the anterior temporal lobes (Bonner et al., 2010; Patterson et al., 2007). Degeneration is observed bilaterally in ATL but is often asymmetrical. Greater left-sided atrophy is associated with lexical-semantic impairments whereas greater right-sided atrophy is associated with disruptions in personality and behaviour (Snowden et al., 1989; Thompson et al., 2003). These patients exhibit a specific impairment of semantic memory in the context of relatively preserved autobiographical, or episodic, memory (Hodges et al., 1992; Snowden et al., 1989; Warrington, 1975). This is in contrast to Alzheimer’s disease in which episodic memory is predominately impacted and there is minimal degeneration of temporal lobes. This dissociation is not perfect, however, as episodic memory can start to degrade over time in patients with semantic dementia (Matuszewski et al., 2009). Critically, the semantic impairments associated with semantic dementia are observed across modalities, across conceptual categories, and in expressive and receptive language abilities. Participants with semantic dementia perform worse on picture naming, picture categorization, color and object recognition, delayed-copy drawing, and single word recognition tasks but have preserved phonology and syntax (Hodges et al., 1992; Patterson et al., 2007; Snowden et al., 1989; Warrington, 1975). As a result, they tend to rely on their perceptual, rather than semantic, systems to recognize objects and slight changes in the perceptual features

of a recognized object can result in a lack of recognition (Graham et al., 2000). Damage to the temporal lobes, in semantic dementia or in other neuropsychological conditions, can also often result in surface dyslexia in which irregular words are not recognized on sight and are instead pronounced, incorrectly, as regular words (Jefferies et al., 2004; Woollams et al., 2007). This multimodal semantic loss appears to be impacted by the familiarity, typicality, and specificity. Impairments are greater for less familiar and less typical concepts (Adlam et al., 2006), and retrieval of superordinate categories (e.g., mammal) tends to be preserved over retrieval of subordinate categories (e.g., grizzly bear) (Warrington, 1975). Taken together, the specific multimodal semantic loss observed in semantic dementia provides strong evidence of ATL involvement in semantic processing.

This is further supported by evidence from other conditions with acquired damage to ATL such as temporal lobe epilepsy (TLE), herpes simplex virus encephalitis (HSVE), and post-stroke aphasia (Lambon Ralph et al., 2012; Schwartz et al., 2009). These studies have shown that semantic impairments are more strongly associated with bilateral ATL damage, with unilateral ATL damage resulting in more mild semantic impairments. Damage to other parts of the semantic system outwith ATL is associated with less domain-general impairments, instead resulting in semantic impairments that disproportionately affect specific semantic categories or particular modalities. Damage to posterior middle temporal gyrus (pMTG), for instance, tends to result in greater impairment in recognition of tools compared to animals (Chen et al., 2017). In visual agnosia, visual object recognition is impaired but tactile recognition is sometimes spared (Devinsky et al., 2008), and a similar modality specific impairment in visual object naming is observed in optic aphasia (Plaut, 2002; Riddoch & Humphreys, 1987). Patients with transcortical sensory aphasia, which often results from lesions in left frontal or parietal areas, display similar semantic deficits as those observed in semantic dementia, but the impairments appear to be limited to semantic control processes rather than a degeneration of conceptual knowledge (Jefferies & Lambon Ralph, 2006). Reduced semantic performance is also reported in TMS studies disrupting ATL activity in neurotypical adults (Binney et al., 2010; Pobric et al., 2007). Integration of these streams of research and the application of neuroimaging methods to study the semantic system (Rogers et al.,

2006) resulted in the prevailing hub-and-spoke neurocomputational account of semantic cognition (Lambon Ralph et al., 2017).

The hub-and-spoke model posits that ATL serves as a hub integrating information via the structural connections of the brain from surrounding sensorimotor spokes to arrive at semantic representations (Chen et al., 2017; Lambon Ralph et al., 2017). The model presumes an embodied cognition framework in which semantic knowledge is acquired through interactions with sensorimotor and perceptual features. There are six proposed spokes: 1) *sound* - auditory cortices, 2) *vision* - occipital cortex, 3) *praxis*, or action knowledge - inferior parietal lobule, 4) *valence* - orbitofrontal cortex, 5) *speech* - inferior frontal gyri, and 6) *function* - posterior middle temporal gyri. There are functional gradations within the ATL – extending outward from the ventral portion of ATL in anterior fusiform which is the transmodal hub receiving equal input from the surrounding spokes. ATL regions proximal to this hub display graded semantic specialization driven by the inputs received from the nearby sensory association cortices. Several white matter tracts terminate within the ATL, and the sites of termination are only partially overlapping, providing additional evidence for this claim (Binney et al., 2012). That ATL is a critical hub for semantic processing is uncontroversial given the strength of the converging evidence across neuropsychological, computational, and cognitive neuroscience studies. The functional gradations of the hub, specialization for varied types of abstract representations which emerge via acquired embodiment in the absence of direct sensorimotor referents (Hoffman, 2016; Hoffman et al., 2018), and engagement in response to naturalistic stimuli remains relatively less explored, however.

## 1.2 Semantic control

The hub-and-spoke model has been further extended to incorporate semantic control, which is the ability to select appropriate, task-relevant conceptual information, inhibit or filter out unrelated or extraneous information, and resolve ambiguities in language (Jackson, 2021). The control network is thought to be separate from the semantic system, although it exerts an influence on the semantic system in directing and constraining the retrieval of semantic knowledge (Lambon Ralph et al., 2017). Within the controlled semantic cognition framework, the interacting systems work cooperatively: semantic concepts are activated within the

transmodal ATL hub and the respective sensorimotor spokes, and an executive mechanism constrains and directs the flow of information to facilitate retrieval of the necessary semantic knowledge (Jefferies et al., 2019; Lambon Ralph et al., 2017; Whitney et al., 2011). The left inferior frontal gyrus (IFG) and posterior middle temporal gyrus (pMTG) are consistently reported in studies of semantic control (Jackson, 2021).

## 2 Opportunities for Advancement

The hub-and-spoke model provides a clear and robust framework predominately focusing on lexical semantics and provides a good account of the comprehension of single words and isolated sentences. This is particularly true for concrete concepts, although theoretical (Barsalou & Wiemer-Hastings, 2005; Hoffman, 2016; Hoffman et al., 2018) and empirical (Arioli et al., 2020; Bucur & Papagno, 2021) accounts incorporating abstract and social concepts are emerging. There remain several opportunities to further refine and extend the model to accommodate other types of conceptual knowledge and comprehension of that knowledge in varied contexts. These opportunities are outlined in the sections below.

### 2.1 *Accounting for divisions within the semantic system*

There is evidence suggesting that semantic memory is comprised of distinct semantic systems corresponding to different conceptual relations (Mirman et al., 2017). Models of semantic memory have predominately focused on feature-based, or taxonomic, relations at the exclusion of event-based, or thematic, relations. Taxonomic relations are based on feature similarity and can be determined from objects presented in isolation. In contrast, thematic relations are based on co-occurrence within an event or scenario, which requires greater consideration of the context that is shared between the concepts. For instance, consideration of the relation between the concepts “cat” and “lap”, which have no feature overlap, requires recalling the event of a cat sitting on an owner’s lap. Although only two concepts are presented, which minimizes the local context, successful recognition of the relation requires knowledge of and access to the context that drove the association. Although a type of concrete conceptual knowledge, thematic relations

may shed light on how abstract and social information, which may similarly emerge from co-occurrence in context (Barsalou & Wiemer-Hastings, 2005; Hoffman et al., 2018), are processed within the semantic system.

Prior research indicates that there is a neural dissociation between the processing of taxonomic and thematic relations (Schwartz et al., 2011; Xu et al., 2018). This work suggests that taxonomic relations are preferentially processed in the semantic hub in ATL, whereas a possible second hub in inferior parietal lobule (IPL) may preferentially process thematic relations. Evidence of a dual-hub architecture is mixed (Mirman et al., 2017) and requires further investigation, including evidence from neuroimaging modalities that provide complementary information to lesion-based and fMRI methods which account for much of the research in this domain.

There is some evidence that the semantic control system is differentially engaged for processing taxonomic and thematic relations, although this may be driven by association strength rather than relation type (Geller et al., 2019; Jefferies et al., 2019; Thompson et al., 2018). In requiring retrieval of relevant contextual information, thematic relations may require control mechanisms whereas taxonomic relations share properties that are embedded within the objects themselves and feature comparison can be done quickly and efficiently.

## 2.2 *Comprehending narratives*

There has been a disproportionate amount of research investigating how the hub-and-spoke model supports comprehension of single words, primarily concrete concepts, with comparatively little research focused on how the semantic system supports comprehension within narratives. As a result, the neural basis of single word comprehension is well-established, but less is known about what it means to hold a representation of a narrative and which neural networks support comprehension.

It is possible, and maybe the presumption, that a neurobiological model developed within artificial laboratory contexts would operate in approximately the same manner in naturalistic settings, but the demands of narrative comprehension suggest otherwise. In order to successfully comprehend the narrative, for instance,

the reader or listener must rapidly retrieve the meaning of the words and integrate them into an evolving mental representation, or situation model, of the events within the narrative (Yarkoni et al., 2008; Zwaan, 2004; Zwaan & Radvansky, 1998). In addition, context changes how word and sentence meaning is constructed (Deniz et al., 2023; Yee & Thompson-Schill, 2016). Unlike single word or sentence studies, newly presented information in a narrative is interpreted with respect to both the local and global events.

Prior studies have examined the neural processing of semantic features in complex narratives. Some of these investigations provide evidence that, in a narrative context, individual concepts still engage the semantic system in expected ways. For example, activation in action planning and execution areas is positively modulated by manipulable nouns presented in written text (Desai et al., 2016). However, several attempts to comprehensively characterize the neural processing of the semantic features of natural language make claims about the organization of the semantic system that ostensibly conflict with the hub-and-spoke framework. These studies have found semantic representations distributed across a much broader, bilateral semantic network (Huth et al., 2016), that is independent of sensory input modality (Deniz et al., 2019; Zhang et al., 2020). This network of regions does not map onto the hub-and-spoke semantic system, though these descriptions of the semantic system may not be mutually exclusive or incompatible (Rogers & Lambon Ralph, 2022). It remains unclear how the lexical and semantic variables that directly informed the hub-and-spoke model are processed when presented in a naturalistic stimulus. Further, there is poor understanding of how more complex dimensions like ambiguity, emotion, and socialness are represented.

The richness of narrative data provides both challenges and opportunities in addressing these gaps. Narratives have multiple, nested feature layers ranging from the words used to construct the narrative to the events that move the story forward (Willems et al., 2020). The complexity of the narrative thus allows for several levels of analysis. As an example, consider the word “*die*” – people tend to rate this word as having a strong, negative emotional valence (i.e., unpleasantness) (Warriner et al., 2013). Now consider the sentence “*How did my father die?*”. The word “*die*” still carries a negative emotional valence, but the conceptual representation, and likely

the emotional impact, is modified by the prior word. Finally, consider this brief passage from *Star Wars: Episode IV – A New Hope*:

**Luke:** *How did my father die?*

**Obi-Wan:** *A young Jedi named Darth Vader, who was a pupil of mine until he turned to evil, helped the Empire hunt down and destroy the Jedi Knights. He betrayed and murdered your father. Now the Jedi are all but extinct. Vader was seduced by the dark side of the Force.*

Even this short exchange highlights some of the challenges of operationalizing semantic content in narratives. In response to Luke's simple question, Obi-Wan provides a brief answer that is rife with information, requiring a significant update to the viewer's situation model of Luke and his familial relations, the interpersonal connections between the characters with the introduction of a narrative antagonist, and the current state of the Jedi order and Vader's role in its demise. A common approach to capturing sentence and passage level content is to aggregate the features of the words in the sentence to approximately estimate the emotional content (Anderson et al., 2017). The lexical and semantic properties of the words in the passage might provide an estimate of the content – “evil”, “destroy”, “betrayed”, and “murdered” may capture the negative emotional weight of the message, for example. This approach does not take narrative context into account, however. Instead, the words are treated as mapping the same meaning regardless of the surrounding narrative content, an approach which has received criticism (Yee & Thompson-Schill, 2016). Subjective sentence-level ratings of the content may provide a more accurate and integrative estimation of the content – that the final sentence is less social than the first sentence allows for investigations of the moment-by-moment fluctuations in social (or other) content. Incorporating even greater context, the entire passage could be considered a single event embedded in the overall narrative and given a rating relative to the surrounding events. The studies described in this thesis quantify the lexical and semantic properties of narratives across these scales – at the word, sentence, and event level – in an effort to comprehensively characterise how the semantic system is engaged across comprehension contexts.

## *2.3 Role of the semantic system in social cognition*

There is considerable neural overlap between the semantic and social cognition brain networks (Adolphs, 2001; Patterson et al., 2007) and, social concepts, like other types of semantic knowledge, are acquired through interactions in social environments in which individuals display or communicate about the behaviours associated with these concepts (Barsalou, 2020; Borghi & Binkofski, 2014). This provides compelling support for the role of semantic cognition in acquiring and accessing social information, and has motivated an account which argues that social cognition requires semantic memory, relying on the neural architecture of the semantic cognition and semantic control systems (Balgova et al., 2022; Binney et al., 2016; Binney & Ramsey, 2020). The same ventrolateral portion of left ATL is engaged by theory of mind processing and non-verbal semantic processing (Balgova et al., 2022), and a recent meta-analysis found that both cognitive systems rely on a shared cognitive control network (Diveica et al., 2021).

It is not clear how social content, ranging from highly social concepts to the need for perspective-taking, is processed within the semantic system in naturalistic contexts. Understanding a highly social moment in a narrative, for example, requires not only understanding the word meanings but also decoding the interpersonal dynamics at play by simulating the mental states of the character(s) (Mar & Oatley, 2008). Research on pragmatics shows that social cognition plays an important role in communication, where context and non-linguistic features convey critical information that is not present in the lexical units or syntactic structures themselves. This pragmatic content allows comprehension of the intended meaning beyond the surface linguistic content (Bambini, 2010; Hagoort & Levinson, 2014) and requires the social cognitive process of mentalizing about the perspectives of the other agents in the environment (Levinson, 2006). Retrieval of the relevant social knowledge - from the names and behaviours of the people we encounter to the concepts used to label those behaviours - may rely on semantic memory. This thesis will investigate the processing of varied social information in narratives and examine the degree to which it is facilitated by the semantic cognition system.

Importantly, social cognition refers to several cognitive abilities ranging from the representation of social information to the wide variety of processes that act on those representations. These processes include reasoning about the minds of others as

well as imitating, empathizing, and sharing attention with others (Frith & Frith, 2008; Happé et al., 2017). Although engaging in these processes requires access to social conceptual knowledge, they are a distinct aspect of social cognition. Such a dissociation is sometimes observed, for instance, in frontotemporal lobar degeneration (FTLD) in which patients may have impaired social conceptual knowledge and preserved understanding of the consequences of social behaviour, or vice versa (Zahn et al., 2017). By using narrative stimuli, the studies described in this thesis predominately capture the representation of social information at the word, sentence, and event level during a passive listening or viewing task. Therefore, these studies examine the representation and access of *social knowledge*. At several points throughout the thesis the term *social process* is used to broadly refer to social cognition, though the studies minimally capture the kind of social processes usually studied in social cognition research and are instead investigating how access to and retrieval of social conceptual knowledge occurs during narrative comprehension and whether it relies on the semantic cognition network.

### 3 Thesis Overview

The empirical chapters in this thesis make reference to each other and form a coherent body of research, but are presented as self-contained journal articles because two are already published, one is a Stage 2 in-principle-accepted registered report, and one will be submitted soon. They are organised by data sets and comprehension contexts, ranging from highly restricted context to multimodal narrative context, rather than by chronological order.

[\*\*Chapter 2\*\*](#) (published as [Thye et al., 2021](#)) describes an investigation of the neural processing of taxonomic and thematic relations using intracranial EEG. It provides the first step towards characterizing comprehension across contexts by using isolated word pairs, thus minimizing the local context within the paradigm, but requiring participants to consider relations that either require (i.e., thematic) or do not require (i.e., taxonomic) consideration of shared context. The results suggest that the semantic system is supported by a dual-hub architecture with specialization for taxonomic relations in ATL and for thematic relations in IPL. The specialization was

time-limited, however, and likely not detectable using fMRI methods which have poorer temporal resolution.

[\*\*Chapter 3\*\*](#) (published as [Thye et al., 2023](#)) presents an investigation of the neural processing of the lexical-semantic content of single words presented in the coherent context of an audiobook. Like the work described in Chapter 2, this study examined brain activation in response to word-level conceptual information, but these words were presented in the global context of the narrative. Both concrete and abstract word-properties were investigated, including the socialness of the words. As a result, this study took advantage of the opportunities to characterise the neural basis of the semantic system during narrative comprehension and to investigate how social processing relies on this system. The results suggest that processing semantic content during narrative comprehension requires a more extensive network than described in the hub-and-spoke model. There is evidence of a hub structure, however, with subregions within the ATL displaying varied sensitivity to semantic and social content as well as narrative moments that provide listeners with an opportunity to reflect on and integrate narrative information.

[\*\*Chapter 4\*\*](#) reports a follow-up study using the same data set as Chapter 3, but instead quantifies analogous content at the sentence-level. This allowed for two extensions of the work outlined in the prior chapters: (1) an investigation of the semantic system using predictors that incorporate more of the narrative context and (2) quantification of non-lexical social information in the narrative such as interpersonal interactions and pragmatic inference. Both social and pragmatic sentence-level content engaged ventrolateral ATL, and there was evidence of functional divisions within ATL that were driven by the different demands of narrative comprehension.

[\*\*Chapter 5\*\*](#) is the Stage 2 manuscript of a [Registered Report](#) that was submitted for Stage 1 review prior to conducting the study described in Chapter 3, but uses similar methods to quantify the word-level variables in an independent data set. The Registered Report format was chosen to constrain the analysis plan and the interpretations given to the results as well as to provide a hypothesis-driven complement to the exploratory analyses described in Chapter 3. In this chapter, the narrative context is multimodal – movies – and both word-level and event-level predictors were used to characterise the semantic system, and social processing

within the system, in response to narrative stimuli. By quantifying the semantic and social event-level content, the narrative context is more closely approximated and accounted for in this study in comparison to the prior chapters. This allowed for a test of multiple levels of social processing, from words to interactions. The results suggest that semantic word-level and event-level content engage a robust comprehension network whereas social words, but not events, engage ventrolateral ATL.

[\*\*Chapter 6\*\*](#) summarises the patterns across chapters, focusing on the cross-cutting implications of the results, and proposes an extension to the current hub-and-spoke model that accounts for comprehension of narratives based on those patterns and the broader literature.

## **Chapter 2**

### **INTRACRANIAL EEG EVIDENCE OF FUNCTIONAL SPECIALIZATION FOR TAXONOMIC AND THEMATIC RELATIONS**

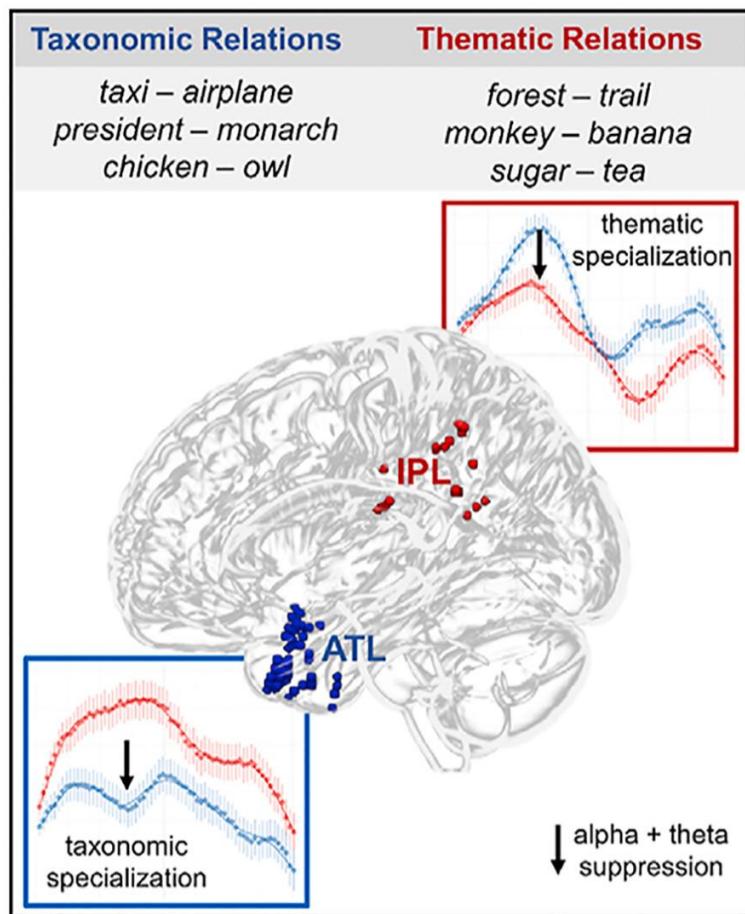
#### **Abstract**

The dual-hub account posits that the neural organization of semantic knowledge is segregated by the type of semantic relation with anterior temporal lobe (ATL) specializing for taxonomic relations and inferior parietal lobule (IPL) for thematic relations. This study critically examined this account by recording intracranial EEG from an array of depth electrodes within ATL, IPL, and two regions within the semantic control network, inferior frontal gyrus (IFG) and posterior middle temporal gyrus (pMTG), while 17 participants with refractory epilepsy completed a semantic relatedness judgment task. We observed a significant difference between relation types in ATL and IPL approximately 600–800ms after trial presentation, and no significant differences in IFG or pMTG. Within this time window, alpha and theta suppression indexing cognitive effort and memory retrieval was observed in ATL for taxonomic trials and in IPL for thematic trials. These results suggest taxonomic specialization in ATL and thematic specialization in IPL, consistent with the dual-hub account of semantic cognition.

#### **Keywords**

*semantic cognition; intracranial EEG; taxonomic; thematic*

## Graphical Abstract



## 1 Introduction

Semantic knowledge is an integral aspect of human cognition. It provides an interpretive framework through which humans interact with their environment and attribute meaning to the objects and events they encounter (Kumar, 2020; McRae & Jones, 2013). Models of semantic memory predominately account for taxonomic relations, focusing on feature overlap to assign concrete concepts into categories within a hierarchical structure (Binney et al., 2010; Lambon Ralph et al., 2017; Patterson et al., 2007). In addition to these taxonomic relations, semantic knowledge also includes thematic relations based on shared context or co-occurrence of events (Binder et al., 2009; Goldwater et al., 2011; Mirman et al., 2017; Mirman & Graziano, 2012; Schwartz et al., 2011). The process of acquiring thematic knowledge is distinct from that of taxonomic knowledge (Estes et al., 2011), and there is a processing time cost to switching between taxonomic and thematic relations (Landrigan & Mirman, 2018). This suggests that these are distinct semantic systems. A recent systematic review found that there are consistent individual differences in strength of taxonomic versus thematic semantic knowledge, that taxonomic and thematic relations make independent contributions to relatedness, and that they have different time courses of activation (Mirman et al., 2017). The systematic review also suggested differences in the neural basis of taxonomic and thematic semantic cognition, but these results were mixed.

There are two opposing accounts of semantic cognition that make different predictions about how taxonomic and thematic knowledge are represented and retrieved in the semantic brain network. The first account, the hub-and-spoke model, posits that the anterior temporal lobes (ATLs), which have been consistently identified as central to semantic cognition (Binney et al., 2010; Lambon Ralph et al., 2017; Patterson et al., 2007; Wong & Gallate, 2012), serve as transmodal hubs integrating information from surrounding sensorimotor spokes to arrive at semantic representations (Lambon Ralph et al., 2010; Rogers et al., 2004). Within the hub-and-spoke model, no neural dissociation would be seen in processing taxonomic and thematic relations. A number of studies have reported such dissociations, however (de Zubicaray et al., 2013; Geng & Schnur, 2016; Kalénine et al., 2009; Kalénine & Buxbaum, 2016; Sass et al., 2009; Schwartz et al., 2011; Tsagkaridis et al., 2014; Wu et al., 2007; Xu et al., 2018). The second theoretical account, the dual-hub

model, suggests that the central role of ATL in models of semantic cognition may be driven, in part, by the over-representation of studies examining taxonomic relations and the difficulty of constructing stimuli and tasks that effectively distinguish taxonomic and thematic relations without introducing differential cognitive demands. In addition, meta-analyses of semantic cognition have identified a possible second semantic hub which supports retrieval of thematic semantic knowledge in the inferior parietal lobule (IPL), comprised of the supramarginal and angular gyri (Binder et al., 2009; Binder & Desai, 2011; Jefferies et al., 2019). The “dual-hub” view suggests that this IPL hub is specialized for thematic relations whereas the ATL hub is specialized for taxonomic relations (Mirman et al., 2017; Xu et al., 2018).

A related extension of the hub-and-spoke-model, the controlled semantic cognition (CSC) framework, additionally highlights the role of a semantic control system, comprised of the inferior frontal gyrus (IFG) and posterior middle temporal gyrus (pMTG) that works alongside the semantic system in directing and constraining the retrieval of relevant semantic knowledge (Jefferies et al., 2019; Lambon Ralph et al., 2017; Thompson et al., 2017; Whitney et al., 2011; Zhang et al., 2020). This semantic control system is especially relevant for retrieving weak semantic relations and selecting task-relevant information. The CSC framework makes two important observations regarding the taxonomic-thematic distinction. First, taxonomically related objects share properties that are inherent to the objects themselves and feature comparison can be done quickly and efficiently. Thematic relations (especially weak relations), however, are not inherent to the objects themselves, so the relevant contextual information must be retrieved, often (though not always) requiring additional semantic control (Thompson et al., 2018; Whitney et al., 2011; Zhang et al., 2020). Second, there is a functional dissociation between the pMTG, which is part of the semantic control system, and the IPL, which is engaged during “automatic” semantic retrieval (Jefferies et al., 2019). The proximity of these regions may have led prior studies to confuse engagement of the pMTG during control-demanding thematic tasks with automatic semantic retrieval supported by IPL. Within the CSC framework, the angular gyrus works alongside ATL in retrieving strong semantic relations and neither region is specialized for processing specific semantic relations, while IFG and pMTG form a semantic control system that is engaged for weak semantic relations or otherwise retrieval-demanding semantic

tasks (Jefferies et al., 2019; Thompson et al., 2017). Support for this position was seen in a MEG study which found that ATL showed a greater response for taxonomic relations whereas thematic relations elicited a stronger response in pMTG. In addition, ATL responded more on strongly related trials, whereas pMTG responded more on weakly related trials, highlighting the role of this region in semantic control (Teige et al., 2019).

The primary aim of the present study was to directly compare the single-hub and dual-hub accounts of semantic cognition by assessing neural responses to taxonomic and thematic relations using a method with high spatial and temporal resolution. Previous studies of semantic cognition have been restricted to neuroimaging methods with limited spatial (centimetre) and temporal (second) resolution, which are not capable of fully exploring the dynamics of the semantic system. Stereoelectroencephalography (sEEG), records directly from an array of depth electrodes implanted throughout the brain and, therefore, captures the spatio-temporal transitions within networks on a much finer neuroanatomical (millimeter) and temporal (millisecond) scale providing an ideal avenue to study semantic processing. A secondary aim was to evaluate whether taxonomic and thematic relations differentially recruit semantic control regions when task demands are matched (i.e., using highly related pairs). This provides an opportunity to directly test the predictions of the CSC framework and leverage the spatial resolution provided by intracranial EEG to dissociate the contributions of pMTG and IPL within the semantic system. The key neural measures in the present study were spectral power in the theta (4-7Hz), alpha (8-12Hz), and high gamma (70-150Hz) bands, which have been used in previous intracranial EEG studies as indices for memory recall (Herweg et al., 2020), active engagement (Klimesch, 2012), and higher-order cognition (Jia & Kohn, 2011), respectively. Specifically, decreases in the theta and alpha power (i.e., alpha suppression) are associated with successful memory retrieval and increased attention, effort, or task engagement (Drijvers et al., 2018; Herweg et al., 2020). Analogous decreases in low frequency power during memory retrieval and attention have been reported across a broad network of left hemisphere language regions (Solomon et al., 2017; Weidemann et al., 2019). Although low frequency power was of primary interest, high gamma band power strongly correlates with BOLD activation

and thus provides complementary information albeit at a much finer spatiotemporal resolution (Engell et al., 2012; Lachaux et al., 2007).

In line with the dual-hub account, it was hypothesized that decreased theta and alpha power would be observed in ATL on taxonomic trials (relative to thematic trials) and in IPL on thematic trials (relative to taxonomic trials). The converse pattern should be observed in the high gamma band: increased power in ATL on taxonomic trials (relative to thematic trials) and in IPL on thematic trials (relative to taxonomic trials). Regarding the secondary aim of investigating the claims of the controlled semantic cognition framework, thematic semantic retrieval was not expected to pose additional control demands especially when stimuli were designed to have minimal semantic control demands, so no differences in processing taxonomic and thematic trials were expected within the semantic control regions (IFG and pMTG). Neither the single-hub nor dual-hub account make claims about the time course of processing taxonomic and thematic relations, so this is left as an exploratory element of this study. The temporal resolution of intracranial EEG provides a unique opportunity to understand how activation within the semantic system unfolds on a millisecond timescale which, when combined with the spatial specificity of the data, can augment current knowledge and yield new predictions about the neural basis of semantic cognition.

## 2 Methods

### 2.1 Participants

Thirty-one patients with refractory epilepsy took part in this study after written informed consent was obtained. All participants were undergoing in-patient phase II video and EEG monitoring to localize seizure onset in preparation for possible surgical resection; all were tested at least 24 hours after implantation of electrodes and were sufficiently recovered from the anesthesia as documented by normal (or at baseline) neurological examination before obtaining consent and performing study procedures. All determinations of the return to normal (or baseline) neurological examination were performed by a neurologist or neurosurgeon not affiliated with the study. SEEG electrode localization was determined by evaluation needs (standard of care) and additional electrodes were not added for the purpose of this study.

Participants were excluded from analysis if they had low accuracy (<60%) in either task condition (n=2), both Full Scale and Verbal IQ in the mildly impaired range (<70) (n=2), seizure activity during the task (n=1), errors in data recording (n=3), or lack of electrodes in the regions of interest (n=6). Exclusion criteria were established prior to data analysis. The final sample for analysis consisted of 17 participants. The demographic and neuropsychological information is provided in **Table 1**. The participant-level electrode coverage within each region of interest is provided in [\*\*Appendix A: Supplemental Table 1\*\*](#). The study was carried out in accordance with protocols approved by the Institutional Review Board at the University of Alabama at Birmingham. All participants signed an informed consent.

**Table 1**

*Participant Information*

	N	Mean (SD)	Range
Age (years)	17	35.75 (8.79)	24-49
Full Scale IQ	16	87.38 (19.09)	61-129
Verbal IQ	17	94.82 (19.27)	63-130
Semantic Fluency	14	17.43 (5.12)	9-24
Accuracy (%)			
<i>Taxonomic Trials</i>	17	83.82 (11.49)	68.75-100
<i>Thematic Trials</i>	17	86.40 (10.88)	62.50-100
Reaction Time (s)			
<i>Taxonomic Trials</i>	17	4.11 (1.87)	1.12-8.47
<i>Thematic Trials</i>	17	3.99 (2.29)	1.21-9.52
Sex (M:F)	6:11		
Race (B:W)	6:11		
	N	No. Channels	Coverage Mean (Range)
ATL	8	56	7 (4-10)
IPL	6	25	4 (1-8)
IFG	16	116	7 (2-12)
pMTG	14	62	4 (1-11)

Note. Semantic fluency scores were derived by asking participants to list as many animals as they could within one minute. N, number of participants; SD, standard deviation of the mean; s, seconds; No., number; M, Male; F, Female; B, Black; W, White; ATL, anterior temporal lobe; IPL, inferior parietal lobule; IFG, inferior frontal gyrus; pMTG, posterior middle temporal gyrus; Coverage Mean (Range), mean number of electrode channels and the range of coverage for participants with electrodes within each region (indicated by N).

## 2.2 Materials

Participants completed a semantic relatedness judgment task that has been used in a previous study with neurologically typical participants (Geller et al., 2019). Critical word pairs were derived from publicly available word norms of taxonomic and thematic relations (Landrigan & Mirman, 2016) and differed in the type of semantic relationship (taxonomic or thematic) and the strength of the semantic relationship (strongly related or weakly related). The stimuli and word properties are available on the project OSF page (<https://osf.io/xtfah/>). Only the strongly related trials were analysed in the current study ([Appendix A: Supplemental Table 2](#))<sup>1</sup>. These strongly related stimuli were previously found to be matched in terms of control demands based on response times, accuracy, and a psychophysiological measure of cognitive effort (i.e., task-evoked pupillary response (TEPR); Geller et al., 2019). Filler trials of unrelated word pairs comprised 50% of the total number of trials. Conditions were matched on word length (in letters, syllables, and phonemes), word frequency (Brysbaert & New, 2009), imageability, and orthographic neighbourhood size.

## 2.3 Procedure

Participants completed an approximately one-hour testing session consisting of four language tasks during continuous sEEG monitoring. Intracranial video-EEG from an array of multi-contact depth electrodes (8-16 contacts, 2 mm contact length, 0.8 mm contact diameter, 1.5 mm inter-contact distance) were recorded using Natus Xltek with sampling at 2 kHz to allow for better processing of the signal.

All tasks were administered in each participant's hospital room via a laptop positioned within arm's reach of the participant on an adjustable table. Task instructions were presented on screen and explained verbally, and participants completed several practice trials prior to beginning each task. During the semantic relatedness task, two words appeared on the screen, and participants were asked to

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<sup>1</sup> Accuracy on weakly related trials was relatively poor across participants ( $M = 73.5\%$ ) and below the 60% threshold for 6 of the 17 participants, which drastically reduces the sample size and makes the data unreliable both statistically (error trials were excluded, so the number of analysed trials would be low) and theoretically (with accuracy close to the 50% chance level for several participants, even the correct responses could be guesses, so it cannot be assumed that the correct semantic relations were retrieved on those trials either).

judge whether the words were related or unrelated. Responses were indicated via the laptop keyboard using the “Z” key for related and the “M” key for unrelated. A total of 128 trials (64 critical trials, 16 in each condition) were presented in random order with an inter-trial interval of 2000ms during which participants saw a fixation cross. Trials were presented within 8 discrete blocks, and participants were given a break after each block. Trial onset signals from the experiment software were converted into TTL pulses by a custom-built Arduino device to mark trial onsets in the EEG data. All tasks were programmed in E-Prime 2.0 software (Psychology Software Tools, 2016).

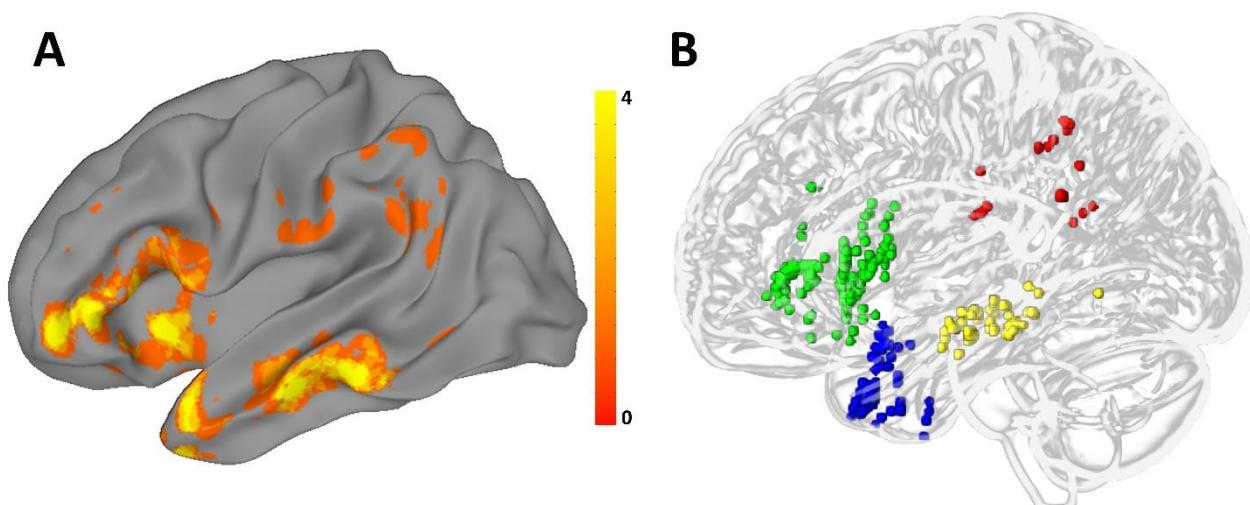
## 2.4 *Data preprocessing*

Participant pre-operative MRI scans were processed through FreeSurfer (Dale et al., 1999) to generate a cortical surface mesh and co-registered with the post-implantation CT scan. Electrodes were manually localized in native space by identifying the centre of the visible artefact on the CT scan using the iElectrodes program (Blenkmann et al., 2017). Electrode coordinates were normalized to template space using the MATLAB-based FieldTrip toolbox (Oostenveld et al., 2011) and referenced to standard atlases using code adapted from Stolk et al. (2018). Electrode locations were visualized by generating a 3mm sphere around each normalized coordinate using AFNI (Cox, 1996).

Signal data were processed in MATLAB 2019a (MATLAB, 2019) using the signal processing and FieldTrip toolboxes. A detailed overview of the pipeline and the code used to run all analyses are available on OSF (<https://osf.io/xtfah/>). Data were segmented into 2500ms windows capturing the trial and baseline period (500ms). Trials were demeaned and line noise around 60Hz (and its 2<sup>nd</sup> and 3<sup>rd</sup> order harmonics) was attenuated with a notch filter. Data were visually inspected, and channels with excessive spiking across trials were removed (n=25). An automated artefact rejection algorithm was run on the z-transformed data (threshold=7), and trials which contained an artefact were excluded from analysis. Data were downsampled to 500Hz and each channel was re-referenced to the median value of the other channels on the electrode shaft. The resulting data were bandpass filtered using a 6<sup>th</sup> order Butterworth filter to separately extract the theta band (4–7Hz), the

alpha band (8–12Hz), and high gamma band (70–150Hz). The Hilbert transform was applied to compute the analytic signal within each of the extracted frequency bands, and the data were smoothed using overlapping sliding windows of 250ms every 30ms and baseline corrected using the percent change from the 300ms prior to the trial onset.

Data were recorded from a total of 1298 electrode channels for the 17 participants included in the analysis, of which 1039 were excluded from analyses due to the presence of excessive artefacts or placement outside of the regions of interest (ROIs). The ROIs were derived using the cortical parcellation of several atlases due to the lack of a clearly defined ATL or IPL region in any single atlas, although there was significant overlap in the region definitions across atlases. The left ATL region was comprised of the middle and superior temporal pole regions within the AAL atlas (Tzourio-Mazoyer et al., 2002), the temporal pole region with the Harvard–Oxford atlas, and the temporal pole region within the Destrieux atlas (defined in participant native space) (Destrieux et al., 2010). The left IPL region was comprised of the supramarginal and angular gyri regions within the AAL atlas and the supramarginal region within the Desikan-Killiany atlas (defined in participant native space) (Desikan et al., 2006). The left IFG region was comprised of the orbital, triangular, and opercular parts of the inferior frontal gyrus in the AAL atlas, and the IFG region within the Brainnetome (Fan et al., 2016) and AFNI Talairach–Tournoux (Lancaster et al., 1997) atlases. The left pMTG region was defined as the posterior division and the temporo-occipital part of the middle temporal gyrus within the Harvard–Oxford atlas. See **Figure 1** for electrode coverage across participants within the regions of interest and the location of the electrodes within each ROI.



**Figure 1. Electrode coverage.** (A) Spatial coverage map illustrating the number of participants with electrodes in the same brain areas. Electrodes which fall outside of the regions of interest are not shown. (B) Electrodes within each region of interest (ATL – blue; IPL – red; IFG – green; pMTG – yellow).

## 2.5 Statistical analysis

Filler, weakly related, inaccurate (14.9%), and slow response ( $RT > 10s$ ; 6.8%) trials were removed prior to analysis. The statistical analyses were conducted using a 2s window starting at stimulus onset. To capture changes in the time course of activation, the data were analysed using generalized additive mixed models (GAMMs; Winter & Wieling, 2016; Wood, 2017). GAMMs have several advantages compared to more widely adopted point-by-point methods: (1) GAMMs are more conservative and do not require a multiple comparisons correction. (2) Complex nonlinear relationships can be modelled flexibly while accounting for variation that may arise across participants, trials, and electrodes. This is especially relevant for modelling the fluctuations in the neural signal over the course of the extracted time window. (3) An autoregressive model component can be included to limit the autocorrelation of errors which poses a significant concern in direct analyses of time series data (Baayen et al., 2018). (4) Of particular relevance for the data analysed here, the GAMM approach of fitting smooth splines is a better representation of the underlying data generating process. In contrast, point-by-point comparisons treat each point as an independent observation. This modelling approach has been applied to pupillometry (van Rij et al., 2019), eye-tracking, and event-related

potentials (Porretta et al., 2017), highlighting the applicability of GAMMs to a variety of non-linear time series data.

A generalized additive mixed model was run for each ROI predicting the log-transformed signal (Smulders et al., 2018) within each frequency band with fixed effects of trial type (taxonomic vs thematic), a general smooth effect of time to model the nonlinear change in the signal across the trial duration, and a smooth over time effect for each trial type (i.e., time course differences between taxonomic and thematic conditions). The random effects structure consisted of a by-participant-electrode factor smooth over time (time course differences between individual participant electrodes) and a random intercept of subject-trial. Individual differences across electrodes within subjects and trials within subjects are thus captured within the model specification<sup>2</sup>. Due to high autocorrelation of the residuals within the time series ( $\rho=.92\text{--}.97$ ), the first-order autoregressive model was accounted for in the model estimation. Smoothing was estimated via restricted maximum likelihood (REML). Model predictions were used to isolate the windows of time where the signal differed by trial type. This was done by calculating the difference curve between the fitted smooth condition terms from the model predictions using simulation-derived simultaneous 95% confidence intervals. The statistical analyses were run in R using the mgcv (Wood, 2004) and itsadug (van Rij et al., 2020) packages. The data and code used to run the analysis and additional details regarding the diagnostic plots and model specification are available on OSF (<https://osf.io/xtfah/>). The diagnostic plots are presented in [Appendix A: Supplemental Figure 1](#).

### 3 Results

There were no significant differences in accuracy ( $t(16)=1.05, p = .31$ ) or reaction time ( $t(16) = -.27, p = .79$ ) between the taxonomic and thematic trials, consistent

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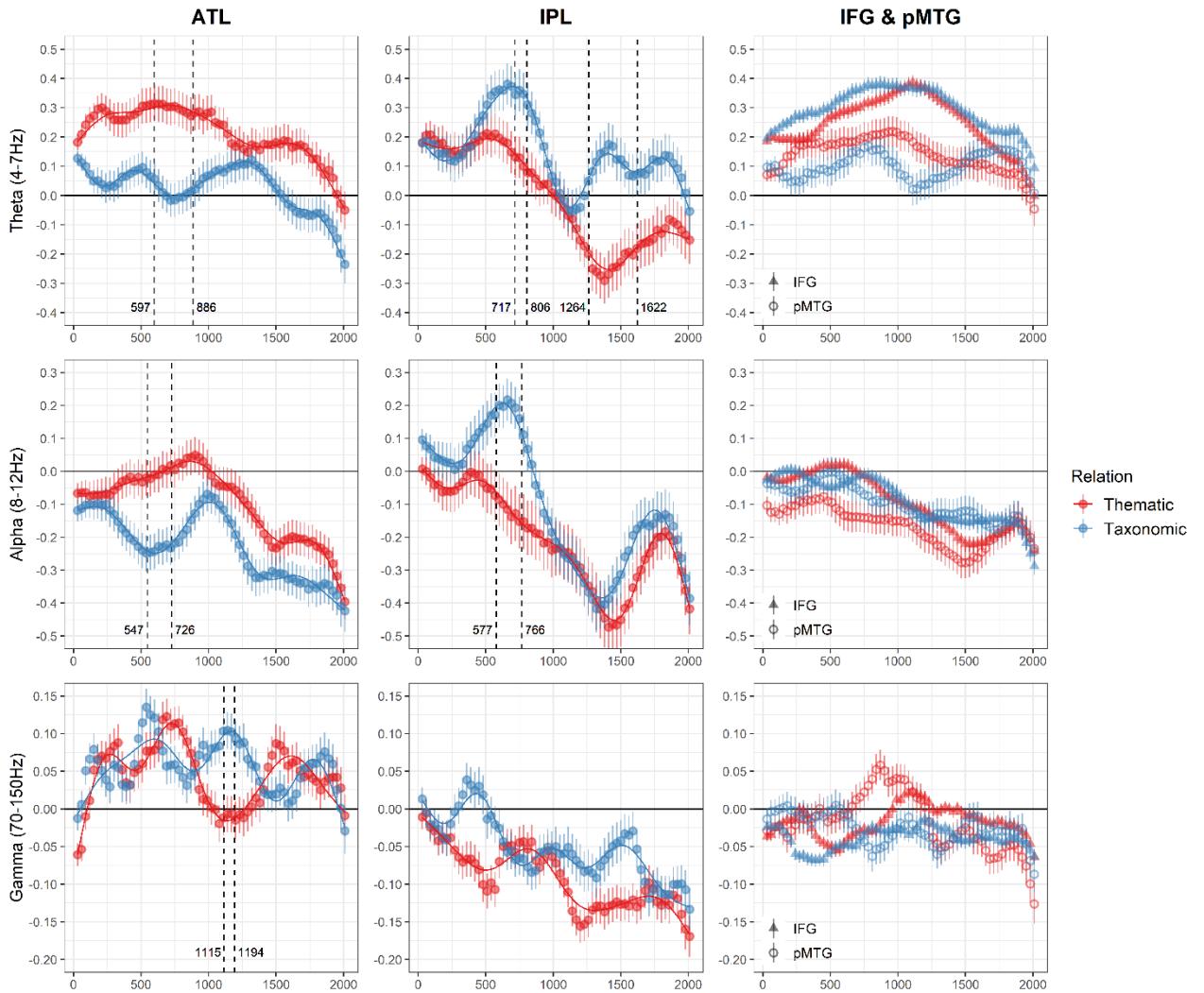
<sup>2</sup> The models were also run with reaction time included as a fixed effect, and the results were the same. Reaction time was not a significant predictor ( $p > .10$ ) in all but one model (alpha band analysis within IFG:  $p = .02$ ). Model comparisons indicated that the models without the fixed effect of reaction time were preferred. Therefore, the statistically preferred models without the reaction time effect are reported here. Additional information on the reaction time analyses are available on the project OSF page.

with previously reported behavioural results from a sample of neurotypical adults (Geller et al., 2019) and further indicating that the control demands were comparable for each condition.

The model estimates for the fixed and random effects are presented in [\*\*Appendix A: Supplemental Table 3\*\*](#). These parameter estimates do not directly answer the research questions, but the model predictions were used to identify time intervals with statistically significant condition differences. **Figure 2** shows the signal time course for each frequency band in each ROI for taxonomic and thematic conditions. The time intervals in which there was a statistically significant difference between conditions are indicated with dashed lines<sup>3</sup>. Time-frequency plots showing the global condition effects across frequency bands are presented in [\*\*Appendix A: Supplemental Figure 2\*\*](#).

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<sup>3</sup> The results from a cluster-based permutation analysis approach largely converged with the results reported here with the exception of additional time windows of significant condition difference due to the less conservative nature of this analysis. Additional information regarding these analyses are available on the project OSF page.



**Figure 2. Signal time course results.** The time course of spectral power for the theta (top row), alpha (middle row), and high gamma (bottom row) frequency bands for ATL (left column), IPL (middle column), and IFG and pMTG (right column). For the semantic control regions shown in the right column, IFG data are plotted with filled triangles and pMTG data are plotted with open circles. Time (0-2000ms post trial onset) is shown on the x-axis and the log transformed signal is shown on the y-axis. Thematic relation trials are shown in red, taxonomic trials are shown in blue, and the time windows with statistically significant differences between conditions are marked by dashed vertical lines.

### 3.1 *Theta*

Within the ATL, theta band power was significantly lower on taxonomic trials compared to thematic trials from 597 to 886ms after the trial onset. The opposite pattern was observed in the IPL with lower theta band power on thematic compared to taxonomic trials from 717 to 806ms and again from 1264 to 1622ms after trial onset. There were no significant windows of time where the signal differed by condition in either IFG or pMTG.

### 3.2 *Alpha*

The pattern of results in the alpha band was similar to the theta band. Within the ATL, alpha band power was significantly lower on taxonomic trials compared to thematic trials from 547 to 726ms after trial onset. In IPL, alpha band power was lower on thematic trials compared to taxonomic trials from 577 to 766ms. There were no significant differences between the conditions across the time course in either IFG or pMTG.

### 3.3 *High gamma*

Unlike the theta and alpha bands, the course of high gamma band power was highly variable, with only a small window of significant difference between taxonomic and thematic trials: greater high gamma band power in ATL on taxonomic trials compared to thematic trials from 1115 to 1194ms<sup>4</sup>. There were no significant differences between the conditions across the time course in the IPL, IFG, or pMTG.

## 4 Discussion

Two opposing theoretical accounts of semantic cognition were examined using intracranial EEG. These accounts make different predictions about the functional specialization for taxonomic and thematic knowledge. The single-hub account predicts equal responses for taxonomic and thematic relations in ATL and no

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<sup>4</sup> Diagnostic plots indicated that the distribution of residuals was heavy-tailed in the gamma models, so these models were re-run using a scaled T distribution. With these models, the condition effect in ATL was no longer significant.

evidence of specialization within IPL. Conversely, the dual-hub account predicts stronger response in ATL for taxonomic relations and in IPL for thematic relations. Differences in the relative reliance on a broader semantic control network were also investigated by examining responses in IFG and pMTG. Using prior norming, behavioural, and psychophysiological evidence (Geller et al., 2019; Landigan & Mirman, 2016), the stimuli were designed to minimise and match control demands for the taxonomic and thematic semantic relation conditions, which presented an opportunity to test whether thematic relations inherently recruit the semantic control system. Based on prior intracranial EEG studies, stronger neural response was operationalised as reduced theta and alpha power and increased high gamma power (Herweg et al., 2020; Klimesch, 2012; Lachaux et al., 2007).

The ATL and IPL showed differential responsiveness to taxonomic and thematic relations in low frequency bands, where reduced spectral power is associated with task engagement and memory retrieval (Drijvers et al., 2018; Herweg et al., 2020; Klimesch, 2012). In ATL, the taxonomic condition response was significantly reduced relative to the thematic condition response from 597 to 886ms in the theta band and from 547 to 726ms in the alpha band. The opposite pattern was seen in IPL, with reduced theta power on thematic compared to taxonomic trials from 717 to 806ms and again from 1264 to 1622ms and reduced alpha power from 577 to 766ms. These results are consistent with the dual-hub prediction of greater ATL engagement in retrieving taxonomic relations and greater IPL engagement in retrieving thematic relations.

The relatively symmetric functional specialisation observed in this study is likely a product of the matched taxonomic and thematic stimuli and task, combined with the high spatial and temporal resolution of sEEG. Other studies that showed converging evidence of functional specialisation have not always found such symmetric effects. For instance, in picture naming, participants usually make more taxonomic errors than thematic errors, possibly because visual features – which tend to be shared among taxonomically-related items – are more salient in a picture-based task. The lesion-symptom mapping analyses in Schwartz et al. (2011) showed that increased rate of taxonomic errors *controlling for rate of thematic errors* was associated with ATL damage and increased rate of thematic errors *controlling for rate of taxonomic errors* was associated with IPL damage. That is, although all participants made more

taxonomic errors than thematic errors, the magnitude of that difference depended on the lesion location.

The timing of the observed effect may also be an important consideration when situating the present results in the broader literature. The specialization observed here was relatively early, transient, and primarily in the lower frequencies – the ATL and IPL hubs showed different degrees of suppression of low frequency (theta and alpha band) oscillations early after trial onset, but then seemed to work cooperatively to retrieve taxonomic and thematic relations. Studies using fMRI may not have been able to capture this transient dissociation given the lack of temporal resolution and may have been primarily capturing high gamma band power, which is more strongly associated with the BOLD signal. For example, a recent fMRI study using representational similarity analysis found that representational patterns in IPL showed approximately equal taxonomic and thematic similarity, while representational patterns in ATL showed much stronger taxonomic similarity than thematic similarity (i.e., Xu et al., 2018). Although both the Xu et al. fMRI study and the current sEEG study provide very clear evidence consistent with the dual-hub account, they do so on the basis of rather different neural signatures.

Alpha and theta suppression were most prominent in both ATL and IPL relatively early in the time course, approximately 550–750ms after trial onset. The time course of activation was largely consistent across the low frequency bands and condition differences occurred at approximately the same time within ATL and IPL. It is important to note that the statistically significant time windows should not be interpreted as qualitatively distinct stages; they identify time points that passed a statistical significance threshold, thus highlighting the time points where the differences were strongest. However, the stimulus-evoked responses evolve gradually, so the adjacent time points outside of the identified windows likely fall just below the statistical threshold. These results do indicate that the differential response is a transient aspect that occurs early in semantic retrieval. Methods with coarser temporal resolution (such as fMRI) would be unlikely to capture these transient differences which underscores the value of using intracranial methods to enhance current neurobiological models of semantic cognition. Across most of the time course, ATL and IPL responded similarly on taxonomic and thematic trials, suggesting substantial coordinated processing between these semantic hubs.

Although neither the single-hub nor dual-hub account make any particular claims about the time course of activation, the transient differential response conflicts with the single-hub CSC framework prediction that ATL and IPL should respond equally to taxonomic and thematic relations under conditions requiring minimal semantic control. The stimuli and task were specifically designed to minimise and match semantic control demands and the lack of condition differences in IFG and pMTG suggest that this was successful. It is important to note that electrode coverage within the most posterior portion of pMTG was limited in this sample of participants, but no condition effect was observed in either semantic control region. Retrieval of strongly related taxonomic and thematic relations did not exert differential demands on the semantic control system.

Within the high gamma band, the taxonomic condition response was significantly higher than the thematic condition response from 1115 to 1194ms in ATL, but no condition differences were seen in either IPL, IFG, or pMTG. Taken together with the theta and alpha band, these results align with the spectral tilt phenomenon reported in studies of human memory wherein decreased power is observed in lower frequency bands (i.e., theta and alpha) with corresponding power increases seen in higher frequencies (>30Hz) (Herweg et al., 2020). Although the time window is relatively brief, this is consistent with the ATL preferentially processing taxonomic relations, though a complementary tilt for thematic relations was not found in IPL and the low-frequency ATL response appears to be more robust. Given the known correspondence between high gamma band power and the BOLD response (Engell et al., 2012; Lachaux et al., 2007), this result may explain the mixed reports of ATL and IPL involvement in fMRI studies investigating taxonomic and thematic relations (Geng & Schnur, 2016; Jackson et al., 2015; Xu et al., 2018).

Previous scalp EEG and MEG studies have attempted to isolate the time course of activation associated with processing taxonomic and thematic relations, although without the spatial resolution provided by intracranial recording. Many of these studies have reported key differences in processing of taxonomic compared to thematic relations. For instance, taxonomic and thematic relations were found to produce distinguishably different N400 amplitudes (Honke et al., 2020), P600 amplitudes were significantly larger for taxonomic compared to thematic items (Savic et al., 2017), and a larger frontal P600 response was observed for taxonomic

compared to thematic relations (Chen et al., 2013). One scalp EEG study reported increased theta power in right frontal regions for thematic relations and increased alpha power over parietal areas for taxonomic relations (Maguire et al., 2010) which is largely consistent with the alpha and theta suppression observed in the current study. It is important to note, however, that scalp EEG and MEG may not be directly comparable to intracranial EEG: these methods consistently produce discrepant results, suggesting that they are capturing different properties of the frequency band. In particular, intracranial recordings capture oscillations in local field potentials that are interpreted as general increases in power when coarsely recorded at the scalp (Herweg et al., 2020). The results of the present study highlight the applicability and potential of intracranial EEG to further current understanding of human cognition.

The functional specialization observed in this study is consistent with the “architectural specialization” hypothesis proposed by Mirman et al., (2017) in which the neural architecture of semantic cognition is divided according to the differential demands of identification and prediction. Identification and categorization of concepts based on features captures taxonomic relations whereas prediction based on temporal regularities of events captures thematic relations (for a related computational implementation see Hoffman et al., 2018). The present data suggest that ATL is specialized for identification, categorization, and taxonomic relations (consistent with extensive prior research, e.g., (Lambon Ralph et al., 2017; Patterson et al., 2007), while IPL is specialized for prediction and thematic relations (e.g., Matchin et al., 2017; van Kemenade et al., 2017; Xu et al., 2018). The emphasis on prediction is consistent with previous evidence indicating that thematic relations are asymmetrical. Semantic retrieval of causal relations (one kind of thematic relations) is facilitated when they are presented in cause-effect order (Fenker et al., 2005). Regularities in sequences of how concepts co-occur in an event may drive asymmetries in semantic association that have been demonstrated in semantic priming (Hutchison, 2002). Although not explicitly tested in this study, altering the direction of thematic (but not taxonomic) relations may result in varied IPL involvement due to increased prediction demands. The transient differential response observed in the present experiment suggests that, in a general semantic relation judgment task with randomly interspersed taxonomic and thematic trials, both hubs were substantively engaged on each trial; however, on taxonomic trials, a

coherent relation was activated in ATL, whereas on thematic trials, the coherent relation was activated in IPL.

## 5 Conclusion

Intracranial EEG was used to investigate the spatio-temporal dynamics of semantic cognition. A neural dissociation in response to semantic relation type was observed in the two major semantic hubs. Early decreases in low frequency power were stronger for taxonomic relations in ATL and for thematic relations in IPL. No difference was found in either semantic control region suggesting equal semantic control demands for strongly related taxonomic and thematic relations. These results are consistent with a dual-hub account in which ATL is functionally specialized for taxonomic relations and IPL for thematic relations, although the transience of the effect suggests close coordination between these two hubs.

# **Chapter 3**

## **THE WORDS THAT LITTLE BY LITTLE REVEALED EVERYTHING: NEURAL RESPONSE TO LEXICAL-SEMANTIC CONTENT DURING NARRATIVE COMPREHENSION**

### **Highlights**

- Narrative comprehension requires rapid retrieval and integration of word meanings.
- Large brain networks respond to word-level lexical-semantic content in an audiobook.
- Ventral ATL was engaged by semantic content, other ATL subregions were not.
- Semantic control network was engaged by infrequent, less semantically diverse words.
- Social content engages semantic network in dorsolateral and ventrolateral ATL.

### **Abstract**

The ease with which narratives are understood belies the complexity of the information being conveyed and the cognitive processes that support comprehension. The meanings of the words must be rapidly accessed and integrated with the reader's mental representation of the overarching, unfolding scenario. A broad, bilateral brain network is engaged by this process, but it is not clear how words that vary on specific semantic dimensions, such as ambiguity, emotion, or socialness, engage the semantic, semantic control, or social cognition systems. In the present study, data from 48 participants who listened to The Little Prince audiobook during MRI scanning were selected from the Le Petit Prince dataset. The lexical and semantic content within the narrative was quantified from the transcript words with factor scores capturing Word Length, Semantic Flexibility, Emotional Strength, and Social Impact. These scores, along with word quantity variables, were used to investigate where these predictors co-vary with activation across the brain. In contrast to studies of isolated word processing, large networks

were found to co-vary with the lexical and semantic content within the narrative. An increase in semantic content engaged the ventral portion of ventrolateral ATL, consistent with its role as a semantic hub. Decreased semantic content engaged temporal pole and inferior parietal lobule, which may reflect semantic integration. The semantic control network was engaged by words with low Semantic Flexibility, perhaps due to the demand required to process infrequent, less semantically diverse language. Activation in ATL co-varied with an increase in Social Impact, which is consistent with the claim that social knowledge is housed within the neural architecture of the semantic system. These results suggest that current models of language processing may present an impoverished estimate of the neural systems that coordinate to support narrative comprehension, and, by extension, real-world language processing.

## **Keywords**

*semantic cognition; narrative comprehension; naturalistic neuroimaging; social cognition*

## 1 Introduction

Comprehending narrative language requires rapidly accessing the meanings of words and integrating the sequence of words into a holistic situation model – a mental representation of the events described (Yarkoni et al., 2008; Zwaan, 2004; Zwaan & Radvansky, 1998). The words within the narrative thus serve as the conceptual building blocks that collectively construct the complex ideas and events from which the gestalt of the narrative emerges. This process relies on semantic memory, which stores the meanings of words and provides a knowledge basis for interacting with and interpreting the concepts and events in the world around us (McRae & Jones, 2013).

Extensive behavioural, neuroscience, and computational modelling work has converged on a hub-and-spoke neurocomputational architecture of the semantic system in which the anterior temporal lobe (ATL) serves as a graded hub that integrates information from sensorimotor spokes (Lambon Ralph et al., 2010, 2017). However, this model was primarily based on data from studies of processing single words, sentences, or simple images depicting word-level concepts (Rogers et al., 2004). It also primarily focuses on concrete object concepts (cf Hoffman, 2016; Hoffman et al., 2018). Whether the semantic system displays this cross-modal hub architecture when processing more naturalistic language is less clear and has motivated recent investigations with natural or narrative language stimuli.

Prior research has established that narrative speech engages a much broader, bilateral network than the largely left-lateralized network observed for processing single words or sentences (de Heer et al., 2017; Huth et al., 2016; Saalasti et al., 2019). Within this broader network are default mode network structures, in particular the precuneus, which have longer temporal receptive windows that track information as it accumulates over time, within the extended timescale of narratives (Jääskeläinen et al., 2021; Lerner et al., 2011). The specific contributions of the semantic system in narrative processing are unclear, but the engagement of broad networks suggests important deviations from the simple hub-and-spoke model of semantic processing. Thus, insights into the semantic system derived from word and sentence processing cannot be straightforwardly extrapolated to the level of complex narratives.

Efforts have been made to characterize the neural processing of semantic features in complex narratives. Some of these investigations provide evidence that, in a narrative context, individual concepts still engage the semantic system in expected ways. For example, activation in left anterior inferior parietal lobule and posterior inferior temporal cortex, areas associated with action planning and execution, are positively modulated by manipulable nouns presented in written text (Desai et al., 2016). However, several attempts to comprehensively characterize the neural processing of the semantic features of natural language make claims about the organization of the semantic system that ostensibly conflict with the hub-and-spoke framework. These studies generate a semantic space comprised of the word embeddings for the words within the natural speech or narrative stimuli and estimate the voxel-wise prediction accuracy for each semantic category. The results suggest that partially overlapping, and maybe distinct (Huth et al., 2016), regions within a distributed, bilateral semantic network display functional specialization for conceptual categories presented in narratives, and this semantic selectivity appears regardless of sensory input modality (Deniz et al., 2019; Zhang et al., 2020). These studies have led to claims that the cortical response to narratives consists of a mosaic of “semantic tiles” that are selective for particular conceptual categories. However, the network of regions identified does not map onto the semantic system described by the hub-and-spoke framework. The subset of the semantic network that displays specialization for concrete categories (i.e., tool, animal), for example, is more left-lateralized whereas the network specialized for abstract categories (i.e., emotion, change) is more right-lateralized (Zhang et al., 2020). Further, within the identified distributed semantic networks, there is limited semantic specialization in lateral temporal cortex, most notably ATL (Huth et al., 2016). This may be driven, in part, by the challenge of detecting reliable signal in this region due to susceptibility artefacts in gradient-echo fMRI (Devlin et al., 2000), a limitation which is overcome in the current study by using data collected with a multi-echo sequence (Lynch et al., 2021).

These descriptions of the semantic system need not be mutually exclusive or incompatible (Rogers & Lambon Ralph, 2022): this category specificity may emerge as a result of interactions with, and may even require, a deep multimodal hub such as the architecture described by the hub-and-spoke framework (Jackson et al.,

2021). A key challenge in adjudicating between the hub-and-spoke and category-specific tile frameworks is that they are derived from very different experimental and analytical strategies. In particular, they differ on two very different dimensions: (1) isolated controlled stimuli vs naturalistic narratives and (2) theoretically derived lexical-semantic variables vs word-level representations (i.e., word embeddings). As a result, it is unclear how the lexical and semantic variables that directly informed the hub-and-spoke model are processed when presented in a naturalistic stimulus. Further, there is poor understanding of how more complex dimensions like ambiguity, emotion, and socialness are represented. The primary goal of the present study is to examine how these complex dimensions – which are typically studied at the single-word or sentence-level – are represented within the semantic system when embedded in a narrative. By using variables routinely studied in well-controlled single-word studies, we can make clear predictions about the behaviour of the semantic system, and, by using a naturalistic stimulus, we can compare our results with prior investigations of natural speech or narrative processing.

The second goal of the present study is to better understand the role of the semantic system in processing social information in naturalistic contexts. The social cognition system broadly supports the decoding and prediction of social behaviours such as mental state inference, perspective taking, empathizing, and moral reasoning (Adolphs, 2009). Social cognition is often treated as independent from the semantic or language processing systems, and there is evidence of dissociation between the broader language network and the social cognitive regions that support theory of mind reasoning (Paunov et al., 2022). However, there are also key points of overlap between the neural systems supporting social and semantic cognition. For example, the ATL semantic hub is consistently implicated in mentalising or theory of mind tasks in social cognition research, as is the temporo-parietal junction (TPJ) region (Frith & Frith, 2006; Monticelli et al., 2021) which overlaps with the inferior parietal lobule (IPL) semantic hub that may be specialised for event semantics (Mirman et al., 2017; Thye et al., 2021; Xu et al., 2018).

Recent theoretical and empirical accounts argue that social knowledge is a type of conceptual knowledge housed within the broader semantic system (Balgova et al., 2022; Binney & Ramsey, 2020). In this view, social concepts (as well as more abstract social reasoning and prediction) require semantic memory, depend on the

same executive control processes to regulate access to their meanings (i.e., “semantic control”), and are supported by the same neural architecture. Meta-analytic and cross-task empirical data suggest that social processing engages the ventrolateral ATL hub within the semantic system and anterior IFG within the semantic control systems (Balgova et al., 2022; Diveica et al., 2021), but these claims have not been tested with naturalistic stimuli.

A complicating factor is that studies of social cognition and semantic cognition typically use very different tasks, such as word (or picture) matching studies for semantic cognition and false-belief theory of mind tasks for social cognition. These types of paradigms are ideally suited for research questions that assume it is possible to isolate a specific cognitive process, and they can provide clear evidence that is minimally confounded by other processing. However, these highly simplified tasks artificially segment and simplify cognition and thus may inadequately capture complex semantic and social processes and underestimate the interdependence between social and semantic processing. The present study uses a single naturalistic task – narrative comprehension – to examine neural responses when input varies simultaneously along social and non-social dimensions.

Another advantage of using narrative stimuli is that findings are more likely to generalise to real-world language processing. When considering generalization of inferences, more emphasis has been placed on sampling participants that generalize to the population than on sampling tasks and stimuli that generalize to real-world cognition (Brunswik, 1949; Yarkoni, 2022). Naturalistic paradigms provide more accurate estimates of real-word cognitive processing than carefully controlled experimental stimuli (Nastase et al., 2020). Despite the increased complexity, and indeed challenge, of extracting signals of interest in naturalistic processing, naturalistic paradigms better reflect the multi-dimensional inputs experienced during brain development and better preserve the statistical regularities that arise in the natural world. They also provide an opportunity to study continuous fluctuations in response to varied levels of a stimulus.

Narrative stimuli also capitalize on the tendency of the human brain and mind to process and engage with the world through a “narrative mode” (Bruner, 1986). For instance, complex information, such as inferring embedded mental states (i.e., a character’s beliefs about one or more characters’ thoughts or intentions), is hard to

decode when presented in a decontextualized and simplified stimulus, but is readily understood in a narrative context (Van Duijn et al., 2015). Narratives provide multiple, nested feature layers ranging from the words used to construct the narrative to the events that move the story forward (Willems et al., 2020). The neural basis for semantic processing of single-word and sentence-level stimuli is fairly well-established, but it is less clear how the regions that support processing of isolated words and phrases are engaged in the context of a larger narrative. Narrative comprehension unfolds continuously over minutes, perhaps even hours, which impacts the retrieval of relevant representations and may require a fundamentally different processing strategy compared to single words or short passages that can be processed in seconds and are unrelated to the preceding and subsequent stimuli.

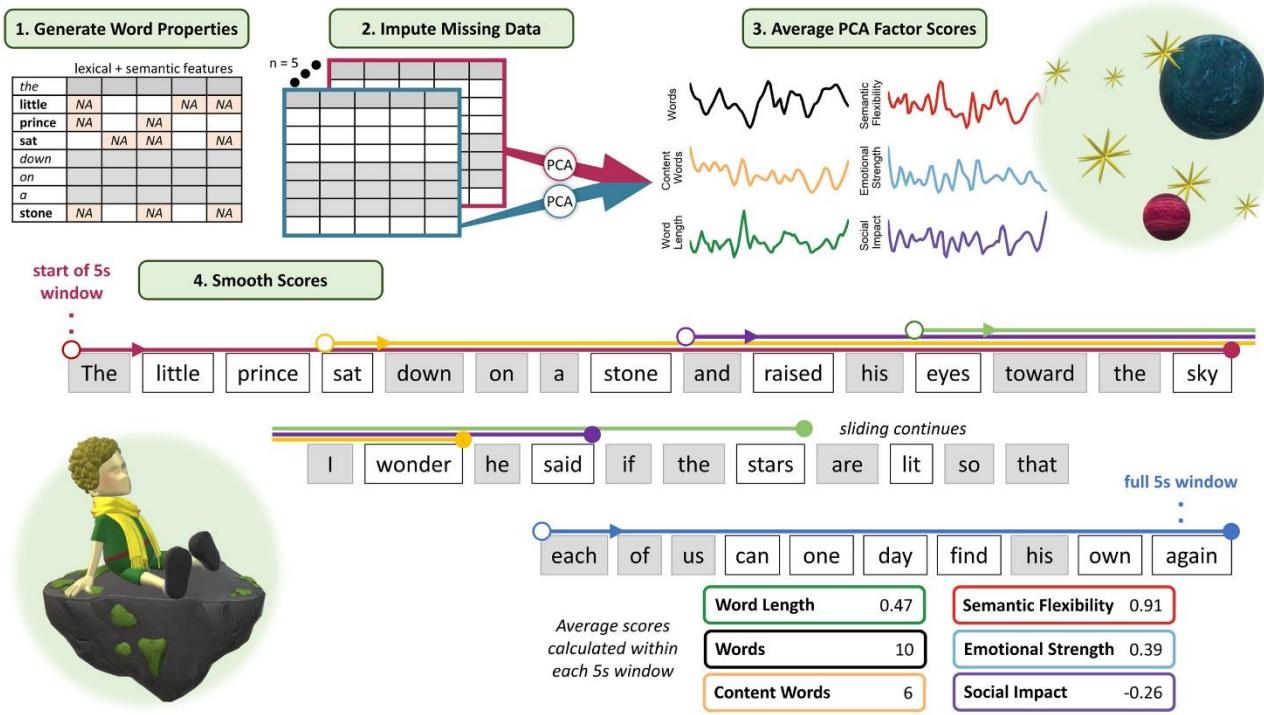
The primary aims of the present study were to examine how word-level lexical and semantic content is processed in the brain when embedded in an auditory story. Auditory story comprehension is an ideal naturalistic paradigm to investigate how the lexical-level building blocks of conceptual knowledge are integrated to build mental models of complex natural situations. New information is constantly provided which builds upon the already established context, so, as the narrative unfolds, meaning is aggregated over time. Newly presented concepts are retrieved with the bias of previously presented information, which is a more ecologically valid test of how the semantic, semantic control, and social cognitive systems are (or are not) cooperatively engaged during real-world comprehension.

To test how the lexical-semantic properties of narratives co-vary with activation across the brain, we analysed fMRI data collected during story listening. The first, exploratory analyses were divided into two complementary aims: (A) to investigate the neural processing of general lexical or semantic content during auditory story comprehension (Aim 1A) and (B) to investigate the neural processing of specific semantic dimensions during auditory story comprehension (Aim 1B). The second, hypothesis-driven aim was to examine engagement of the semantic, social, and semantic control networks in processing varied semantic concepts (Aim 2). It was expected that fluctuations in content words would capture general increases or decreases in semantic content, which would co-vary with activation in the semantic network; in particular, the semantic hub within the ATL. An increase in narrative ambiguity was expected to engage the semantic control network, specifically left

inferior frontal gyrus, and portions of the semantic network. Finally, social content within the narrative was expected to modulate the social cognition network (right IPL and superior frontal gyrus) along with portions of the semantic (ventrolateral ATL and left IPL) and semantic control systems (anterior IFG).

## 2 Methods

This study uses fMRI data from the *Le Petit Prince* dataset, in which 48 participants listened to the same auditory story (Li et al., 2022). **Figure 1** shows a schematic of the analysis approach. In order to isolate both general lexical-semantic content (Aim 1A) and specific semantic dimensions (Aim 1B) within the narrative, various lexical-semantic word properties were generated for the critical words and entered into a principal component analysis to extract a smaller set of latent underlying properties. The factor scores were adjusted for total number of words and averaged within 5 s bins, then used in parametric modulation analyses to examine how neural activity relates to increases or decreases in each lexical-semantic property. To understand network engagement in processing each property (Aim 2), a subset of the results were compared with maps of the semantic, social, and semantic control networks derived from meta-analyses. The sections below provide additional detail regarding how the data were generated and analysed.



**Figure 1. Schematic of the pipeline used to generate modulator variables. (1)**

Word properties were generated for each open class word (bolded) in the transcript. Missing values are indicated with red shading and NA. Closed class words are italicized and their word properties are shaded in grey. (2) Missing values were imputed for open class words, resulting in 5 complete datasets. PCA was run on each dataset separately, and (3) factor scores were averaged together. (4) Smoothed factor scores were generated by averaging values within 5 s windows. An overview of the sliding window approach is depicted using differently coloured windows. The start of each window is indicated with an unfilled circle, and the end of a window is indicated with a filled circle. Open class words, which had factor scores, are in white boxes and closed class words with no ratings are indicated with grey boxes. The number of content words was determined by the number of words with ratings (i.e., words in white boxes) within each window. The bottom row shows the average scores calculated from the content words in a 5 s window.

## 2.1 Dataset

The data were selected from the *Le Petit Prince* dataset (version 1.0.4, <https://openneuro.org/datasets/ds003643/versions/1.0.4>) (Li et al., 2022). The English-speaking participants gave written informed consent prior to participation and were paid, in accordance with the IRB guidelines of Cornell University.

Participants listened to the 94-minute English version of the audiobook, *The Little Prince*, during MRI scanning. The audiobook was presented to participants across nine approximately 10-minute functional runs. After each run, participants answered a series of comprehension questions about the excerpt they had just heard.

The MRI acquisition parameters and pre-processing pipeline are outlined in the paper describing the dataset (Li et al., 2022). Briefly, anatomical data were skull-stripped and spatially normalized to the same stereotaxic space (MNI). Functional images were processed through a standard pre-processing pipeline which included slice-time correction, despiking, co-registration to the anatomical image, and normalization to MNI space. Functional images were acquired using a multi-echo EPI sequence and multi-echo independent component analysis was used to remove noise and motion artefacts. Although raw data were provided for 49 English-speaking participants, the pre-processed data were missing for one participant, resulting in a final sample of 48 participants (29 female;  $M_{age} = 21.33$ ).

## 2.2 Generation of lexical-semantic properties

The transcript of the audiobook with the onset time of each word was made available with the dataset, and we generated a range of psycholinguistic properties for the open class words. Open class words were selected for analysis because they carry more semantic information as opposed to closed class words which have a fixed meaning and predominately serve grammatical functions. Words that can be used as *both* closed and open class were retained. The following word properties were generated using the English Lexicon Project database (Balota et al., 2007): number of letters, number of phonemes, number of phonological neighbours, number of orthographic neighbours, word frequency, concreteness (Brysbaert & New, 2009), semantic neighbourhood density, semantic diversity (Hoffman et al., 2013), emotional valence (i.e., pleasantness), emotional arousal (i.e., intensity), and emotional dominance (i.e., control) (Warriner et al., 2013).

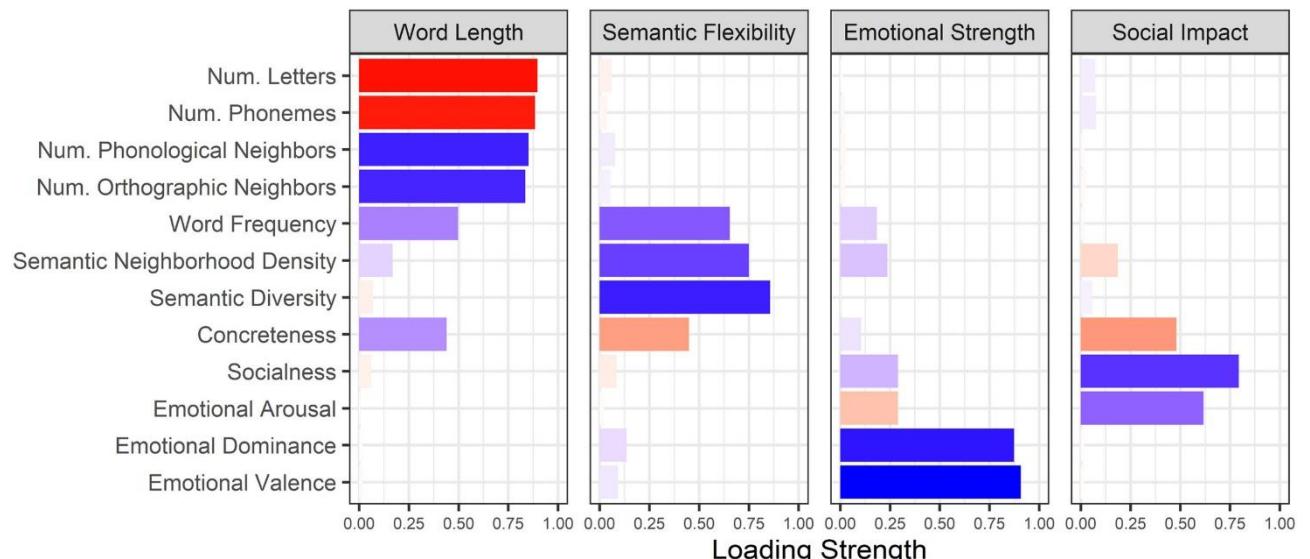
Socialness values were derived from a prior norming study conducted at the University of Alabama at Birmingham. The candidate words came from a study on the social-desirability of personality terms and the Glasgow norms (Hampson et al., 1987; Scott et al., 2018). After filtering to select words with low concreteness and

imageability, a random subset of 688 total words were selected and used for socialness norming. A total of 68 participants were asked to rate the socialness of 344 words (half of the total set) on a scale from 1 (not social) to 5 (very social). Participants were instructed that a word is social if it describes interpersonal behaviours, motivations, intentions, or characteristics. The socialness values of the words in *The Little Prince* were extrapolated by taking a weighted average, using cosine similarity, of the 10 closest semantic neighbours within this set of social norms. This k-nearest neighbour approach to estimating semantic ratings from word associations has been previously used with emotion-based ratings (i.e., valence, arousal, dominance), and the mean calculation was similarly restricted to the 10 nearest neighbours (Meersmans et al., 2020).

Part of speech tags, generated using the Stanford parser and included with the timestamped transcripts, were used to select open class words (i.e., nouns, proper nouns, verbs, adjectives, adverbs, numbers) and remove closed class words (i.e., pronouns, determiners, auxiliary words, adpositions, particles, conjunctions, interjections). The open class word properties were combined with a larger corpus of open class words ( $n=6410$ ) from the movie transcripts of a different publicly available neuroimaging dataset (Naturalistic Neuroimaging Database; Aliko et al., 2020). This was done to make data imputation and the generation of factor scores more robust and less influenced by the relatively small, and possibly idiosyncratic, corpus derived from a single audiobook. Missing data were imputed using the multiple imputation by chained equations approach (van Buuren & Groothuis-Oudshoorn, 2011).

The word properties were entered into a principal component analysis (PCA) with varimax rotation. The four-factor result accounted for 73% of the variance, with factors corresponding to Word Length (e.g., number of letters and phonemes, number of phonological and orthographic neighbours), Semantic Flexibility (e.g., semantic diversity, semantic neighbourhood density, frequency), Emotional Strength (e.g., emotional valence, emotional dominance), and Social Impact (e.g., social content, emotional arousal), which accounted for approximately 29%, 17%, 16%, and 11% of the variance, respectively (**Figure 2**). These labels were selected based on the word properties that most strongly loaded on each factor. However, it is important to note that these labels and properties reflect the single word level, where these word properties are defined and often studied, but in the present study these

properties may be influenced by the narrative context. The Semantic Flexibility factor, for instance, is driven by semantic diversity, frequency, and concreteness, which would tend to increase or decrease the ambiguity of isolated words. At the narrative level, the ambiguity of semantically diverse words is at least partially resolved by the context of the sentence. Similarly, the emotional connotations of a word can vary depending on its context. Alternative “narrative level” labels would require *a priori* theorizing about the combinatorial processing required for a given word property. Furthermore, although the narrative context can modulate these properties, they should remain reliable when considered over the course of an entire story. For these reasons, the single word factor labels are retained here to investigate how standard lexical and semantic variables are processed when embedded in a narrative.



**Figure 2. Factors derived from PCA on word property values.** Positive (blue) and negative (red) loadings are shown for each factor. The strength of the loading is indicated by the length and colour saturation of each bar. Num., Number.

The Emotional Strength factor scores were such that higher scores indicated more positively valenced and dominant words whereas negative scores indicated negatively valenced words. To capture valence extremity (i.e., high versus low valence rather than positive versus negative valence), the absolute values of the

factor scores were used in the analysis. Examples of words with high positive and negative scores on each of the factors are provided in **Table 1**.

**Table 1**

*Example words and windows with high positive and negative factor scores*

	Word Length	Semantic Flexibility	Emotional Strength*	Social Impact
<b>Words</b>				
Positive	<i>man rat say</i>	<i>other many again</i>	<i>die dangerous tragedy</i>	<i>excited charming laugh</i>
Negative	<i>misunderstandings contradictory unfortunately</i>	<i>lamplighter footstool geographers</i>	<i>then offer seen</i>	<i>chimney sheet mushroom</i>
<b>Windows</b>				
Positive	<i>...you can see yourself this is not a sheep it is a ram it has...</i>	<i>I am from everything is very small there will certainly be enough...</i>	<i>...it is nice to have had a friend even if you are about to die...</i>	<i>...very carefully then I am happy and all the stars laugh sweetly...</i>
Negative	<i>...on his discovery at an international astronomy conference but...</i>	<i>...to them of boa constrictors nor of primeval forests nor of the stars...</i>	<i>... I have your sheep and I have the box for the sheep...</i>	<i>...as a tree falls there was not even any sound because of the sand...</i>

Note. \*using absolute value transformed scores. The top part of the table shows words with the highest positive (first row) and highest negative (second row) ratings. The bottom part of the table provides examples of the words that fell within one of the top ten smoothed windows with the highest positive (first row) and highest negative (second row) averaged values.

## 2.3 Smoothed language predictors

Smoothed factor score time courses for the story were generated by averaging values within 5 s windows sliding every 1s<sup>1</sup>. The average was calculated by summing the factor scores of the words within the window and dividing by the number of words with ratings (as opposed to the total number of words). A 5s window was chosen because word boundaries are inconsistent in natural speech, and co-articulation combined with the context of the preceding words means that words are often readily anticipated. Modelling meaning at the word level would result in an imprecise or artificial word boundary. This problem is exacerbated by the variable hemodynamic response across brain regions, with estimated time-to peak differences of 1–2.5s (Handwerker et al., 2004) which is an average of 2–4 words in this narrative. The window approach allows treating words as cues to meaning (Lupyan & Lewis, 2019) rather than as mappings to individual concepts. Defining meaning within a larger temporal unit allows integrating those cues without creating artificial boundaries between the words or committing to isolated word meanings. Similar window averaging or down-sampling approaches have been used in prior studies of narrative comprehension (Deniz et al., 2019; Wehbe et al., 2014, 2021; Wu et al., 2022; Yarkoni et al., 2008).

Window onset times were referenced to the beginning of each functional run (i.e., restarted at 0), and each functional run was processed separately so as not to smooth across consecutive runs. This resulted in the final time window within each run being slightly less than 5s. Example windows with high positive and negative averaged factor scores are provided in **Table 1**. In addition to smoothing the factor scores, the number of words (open and closed class words) and the number of content words (open class words) were calculated for each window to provide an

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<sup>1</sup> At the request of a reviewer, we also ran the factor scores analysis at the subject-level without the sliding window approach, instead modelling the onset and duration of each word. This was done using duration modulated amplitude modulation analyses with word duration and the unsmoothed factor scores as inputs into the model. The correspondence between the subject-level statistical maps was high ( $r = 0.74\text{--}0.95$ ) suggesting that the sliding window approach produces approximately similar results and circumvents potential concerns with modelling word-level variables with sub-second durations ([Appendix B: Supplemental Figure 1](#)).

estimate of the amount of general lexical content and semantically-laden content, respectively.

The number of words was variable across the 5s windows, with a range from 4 to 24 words. The number of words within windows, and in particular the number of closed class words without ratings, co-varied with the averaged factor scores in a non-uniform manner. This was most pronounced for the Word Length and Semantic Flexibility averaged factor scores and was driven by the fact that (1) windows with high positive scores on both of these factors tended to include shorter, more frequent words, (2) audiobooks present the narrative at a fairly consistent rate so windows with several short words tend to have more words overall, and (3) closed class words tend to be short and frequent but were not accounted for in the mean calculation because they do not have ratings. Windows in which there were more words overall were thus likely to both receive higher positive Word Length scores (correlation with number of words:  $r = 0.25$ ) and Semantic Flexibility scores (correlation with number of words:  $r = 0.20$ ) as well as to have more closed class words (with no ratings) (correlation with number of words:  $r = 0.79$ ). This created a potential confound where high positive scores for these factors were coming from windows that simply had more words rather than isolating the properties of interest (i.e., length or flexibility). To account for this, residuals were extracted from independent linear models predicting each averaged factor score from number of words. These residual scores after controlling for number of words were then used for analysis.

## 2.4 *Parametric modulation analyses*

To examine how these smoothed language predictors co-vary with activation across the brain, two regression models predicting the hemodynamic time course were run in AFNI (Cox, 1996). The first model, capturing the amount of content, included the word quantity variables (number of words and content words) as parametric modulators. The second model, capturing the type of content, included the smoothed residual factor scores as parametric modulators. All variables were mean centred prior to analysis. The 9 functional runs were first scaled such that each voxel had a mean of 100 and then concatenated to generate a single time course for

each participant. The durations of the modulators were modelled as 1-second blocks.

The group-level statistical maps were corrected using equitable thresholding and clustering (ETAC; Cox, 2019) implemented for each modulator separately with the following parameters: 1-sided t-tests with spatial clustering based on voxel faces touching (i.e., NN=1) and 1% false positive rate. The more traditional threshold-based cluster correction approach is presented in the supplemental materials ([Appendix B: Supplemental Figure 2](#)). Participant functional data were used as inputs to generate a mean, binarized mask within which the permutations were conducted. For each modulator, the resulting binary masks indicating which voxels survived the multi-thresholding process were applied to the Z-score group-level stats map for positive and negative associations separately.

## 2.5 *Network engagement*

Brain network definitions were derived from coordinate-based activation likelihood estimation (ALE) analyses of social cognition (Diveica et al., 2021) and semantic cognition and semantic control (Jackson, 2021) (see **Figure 5**). The semantic and semantic control network maps were derived from a meta-analysis of semantic control that included over 120 contrasts capturing semantic control and over 400 contrasts capturing the broader semantic cognition network (Jackson, 2021). This more inclusive network was intended to capture *any* semantic processing, including effortful or controlled processing, and, as a result, had considerable overlap with the semantic control network. The control network was subtracted from this broader semantic network to isolate an automatic semantic network. These network maps had significant convergence with the maps generated in a separate ALE analysis (Diveica et al., 2021). The social cognition network was defined by examining the convergence of ALE generated network maps across theory of mind, trait inference, empathy for pain or affective states, and moral reasoning. To identify a cross-task social cognition network, areas of overlap within at least two of these domains were retained in the final network definition.

To examine how our results mapped onto the social, semantic, and semantic control networks, likelihood ratio metrics were calculated that quantified the overlap

between each significant cluster in our results and each brain network. The numerator of the ratio was the number of voxels in the cluster that fell within a given network divided by the total number of voxels in the cluster (i.e., percent of the cluster contained within the network). A value of 1 indicates that the entire cluster fell within the network, whereas a value of 0 indicates that none of the cluster fell within the network. Importantly, this value does not account for the size of the network (or brain). To do this, the denominator took the number of network voxels outside the cluster divided by the total number of voxels outside the cluster (i.e., percent of network non-overlap relative to the rest of the brain).

$$Ratio = \frac{(Result \cap Network)/(Result)}{(Network \notin Result)/(Voxels \notin Result)}$$

This quantified the likelihood of result voxels falling within the network compared to voxels outside the result. Values greater than 1 indicate that voxels within the result are *more likely* to belong to the network (compared to voxels outside the result), whereas values less than 1 indicate that voxels within the result are *less likely* to belong to the network (and voxels outside the result are more likely to fall within the network). The strength of the evidence of network engagement is thus captured by the magnitude of this likelihood ratio value. This likelihood ratio has the benefit of being more readily interpretable and accounting for both the size of the result cluster and the size of the network. This measure was developed to overcome limitations of other measures such as percent overlap, which ignores the amount of non-overlap, or Dice similarity coefficient, which accounts for the amount of non-overlap but generates a less transparent metric for cross-network comparisons. In the latter case, a coefficient of 0.10 for the social or semantic control networks could occur with fewer overlapping voxels than the same coefficient for the semantic network (which is over 1.6 times larger than the other networks). The likelihood ratio metric calculated here has the advantage of having the same interpretation across networks, which facilitates communicating and interpreting the results. All analysis code, study materials, and supplementary information are available on Open Science Framework (<https://osf.io/u54dr/>).

### 3 Results

#### 3.1 General lexical and semantic content

To investigate the differences between the neural processing of general lexical content compared to semantically-laden content, the scores for the Word Length factor are presented alongside the effect of the number of words and number of content words regressors in **Figure 3**. The detailed cluster information is presented in **Table 2**.

##### 3.1.1 Word Length

An increase in words that were shorter, more frequent, and more concrete (indicated by positive Word Length scores) was associated with activation in bilateral inferior frontal gyri, superior medial gyri, precentral gyrus and supplementary motor area, left middle frontal gyrus, a portion of the right anterior superior temporal gyrus (including temporal pole), right middle temporal gyrus extending posteriorly into supramarginal gyrus, and a small posterior portion of the left inferior temporal gyrus. The likelihood ratios were the largest for the semantic control network: the voxels in four of the five clusters were over twice as likely to fall within the control network compared to voxels outside each cluster (likelihood ratios: 2.54 – 24.31).

Engagement of the control network was most prominent for the largest cluster with the peak voxel in the left inferior frontal gyrus and for the smallest cluster with a peak voxel in left inferior temporal gyrus. These clusters also engaged the semantic network (likelihood ratios: 3.26 and 8.20, respectively), and, given the lack of overlap between these networks, it was the voxels that fell outside the control network that engaged the semantic network. The voxels in the right medial temporal pole cluster (which included temporal pole and inferior frontal regions) and the right supplementary motor area cluster (which included superior medial gyrus) were both more than six times as likely to fall within the social network than the voxels outside the clusters (likelihood ratios: 6.42 and 6.64, respectively).

An increase in longer, infrequent, and less concrete words (indicated by negative Word Length scores) was associated with increased activation in bilateral auditory cortices and surrounding regions including portions of the insular cortex and superior temporal gyri, postcentral gyrus, portions of right inferior and superior parietal lobule,

posterior cingulate cortex, and precuneus. There was minimal engagement of the semantic, social, or semantic control networks (max likelihood ratio: 1.31).

### 3.1.2 Number of words

An increase in total number of words was associated with increased activation in left anterior inferior and superior temporal lobe extending posteriorly into middle and superior temporal gyri and auditory cortex and left angular gyrus, right anterior inferior temporal gyrus, right auditory cortex including a portion of superior temporal gyrus, a portion of right angular gyrus, middle and superior frontal gyrus, posterior cingulate cortex, precuneus, and cerebellum. These results engaged shared and distinct regions within the semantic and social networks. The largest cluster included left inferior, middle, and superior temporal gyri and angular gyrus, and most prominently overlapped with the semantic network (likelihood ratio: 11.85). Additional semantic network engagement was seen for the clusters with peak voxels in the left superior frontal gyrus and right Heschl's gyrus – voxels in these clusters were approximately three times more likely to fall within the semantic network compared to voxels outside the clusters. There was considerable engagement of the social network for these clusters as well, partly because the semantic and social networks overlap in middle temporal and frontal areas. Evidence of additional social network involvement outside of overlapping areas was seen in the precuneus/cingulate and right angular gyrus clusters (likelihood ratios: 6.10 – 12.75). There was minimal activation in the semantic control network (max likelihood ratio: 0.87).

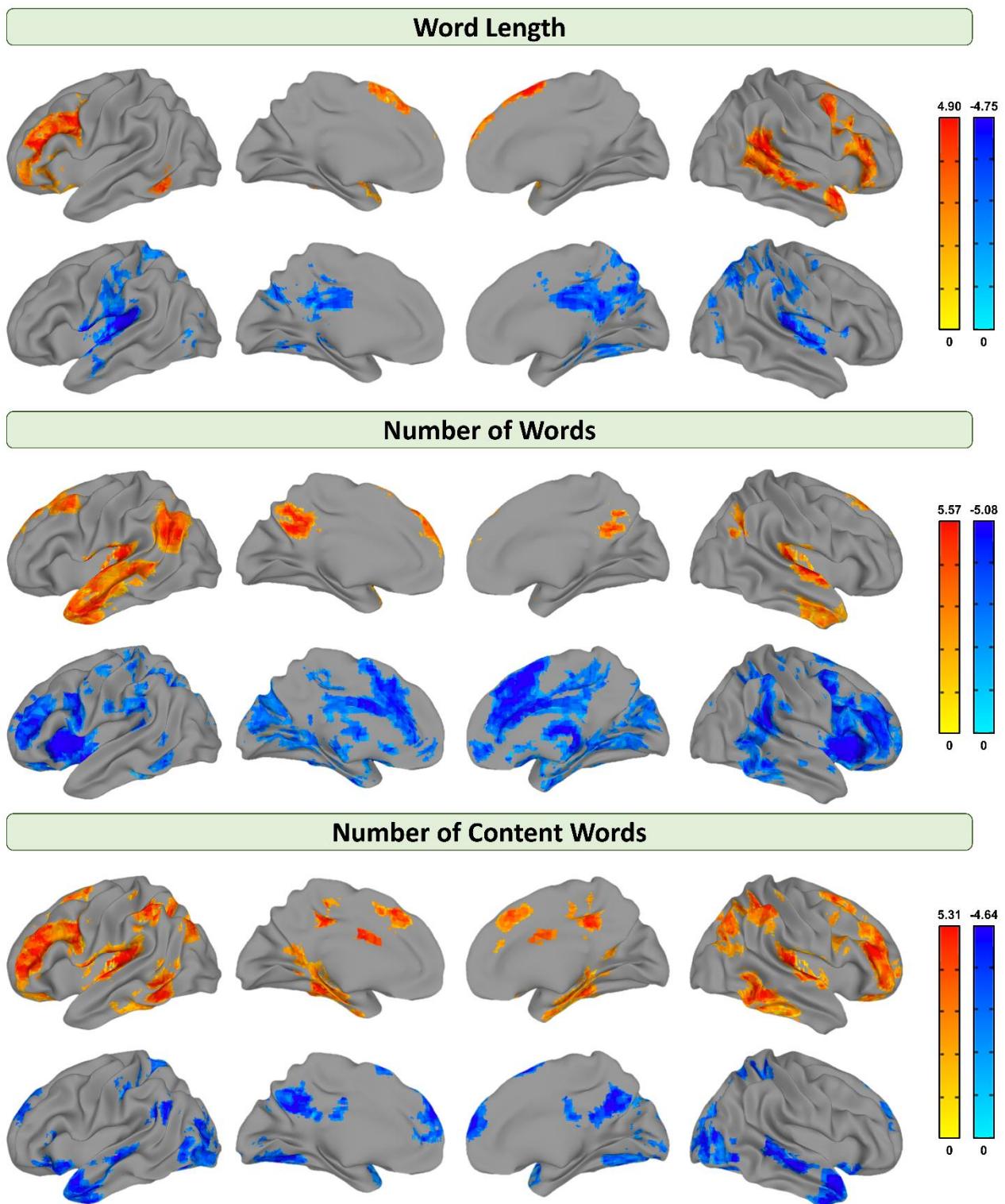
A decrease in total number of words was associated with widespread activation in bilateral inferior frontal regions, insula, anterior to posterior cingulate cortex, a bilateral posterior portion of the inferior and middle temporal gyri, portions of bilateral inferior parietal lobule, and precuneus. The full result had moderate overlap with the semantic control network (likelihood ratio: 2.66), but minimally engaged the semantic or social network (likelihood ratios: 0.62 and 0.50, respectively).

### 3.1.3 Number of content words

Increased number of content words, capturing general semantic processing demand, was associated with increased activation in bilateral auditory cortex,

inferior, middle, and superior frontal gyri, inferior, middle, and superior temporal gyri, fusiform gyri, portions of inferior parietal lobules, and middle cingulate cortex. The clusters with peak voxels in left inferior temporal gyrus and left Heschl's gyrus were over 2 to 3 times more likely to fall within the semantic network compared to voxels outside the cluster (likelihood ratios: 3.74 and 2.67, respectively). The largest cluster, with a peak voxel in right inferior frontal gyrus, overlapped considerably with the semantic control network (likelihood ratio: 8.76). There was minimal overlap between the remaining clusters and the semantic, social, and semantic control networks.

Conversely, as the number of content words decreased there was increased activation in superior frontal gyrus, the orbitalis portion of the inferior frontal gyri, bilateral anterior temporal poles, inferior and middle temporal gyri and fusiform gyri, left inferior parietal lobule, precuneus, occipital gyri, and cerebellum. The clusters containing bilateral inferior, middle, and superior temporal gyri, bilateral temporal poles, supramarginal gyrus, and angular gyrus had considerable overlap with the semantic network (likelihood ratios: 4.04 – 9.39) and the social network (likelihood ratios: 5.53 – 13.03). The clusters with peak voxels in precuneus and left supplementary motor area also engaged the social network (likelihood ratios: 2.39 and 12.13, respectively). Across the full result, the control network was minimally engaged with the only overlap occurring in the cluster with the peak voxel in left inferior temporal gyrus (likelihood ratio: 5.63).



**Figure 3. Word Length, Number of Words, and Number of Content Words**

**Results.** The Z-score statistical maps are shown for each result with the range of values indicated by the associated colour bars. Warm colours (yellow to red) indicate regions with a positive correlation with the score, and cold colours (cyan to dark blue) indicate regions with a negative correlation with the score.

### **3.2 Varied semantic concepts**

The next exploratory aim was to assess the neural response to diverse kinds of semantic information; namely, ambiguous, emotional, and social content. The whole-brain results for each of the variables are presented in **Figure 4** and detailed cluster information is presented in **Table 2**.

#### **3.2.1 Semantic Flexibility**

More frequent, less concrete, and more semantically diverse words (indicated by positive Semantic Flexibility scores) were associated with activation in multiple demand network regions in the left anterior inferior temporal gyrus, middle cingulate cortex, occipital cortex, and left superior frontal gyrus. The cluster with a peak voxel in left inferior temporal gyrus overlapped with the semantic and social networks (likelihood ratios: 4.40 and 3.36, respectively), but the remaining regions had minimal overlap with the networks (max likelihood ratio: 0.38).

Conversely, increased infrequent, concrete, less semantically diverse language (indicated by negative Semantic Flexibility scores) was associated with activation in bilateral inferior, middle, and superior frontal gyri, precentral gyrus, inferior, middle, and superior temporal gyri, fusiform gyrus, left inferior parietal lobule, and cerebellum. Several of the results clusters (4 out of 7) were over twice as likely to fall within the control network compared to voxels outside each cluster (likelihood ratios: 2.01 – 24.16). This overlap occurred in bilateral inferior frontal and posterior inferior temporal areas. The largest cluster, which contained left temporal areas, fusiform gyrus, and inferior parietal lobule, had considerable overlap with the semantic network (likelihood ratio: 9.28). The right inferior frontal gyrus cluster, which included middle frontal and precentral gyri, also overlapped with the social network (likelihood ratio: 3.64), and this was the only evidence of engagement of the social network by Semantic Flexibility.

#### **3.2.2 Emotional Strength**

Increases in Emotional Strength were associated with activation in left superior medial and frontal gyri, right inferior temporal and fusiform gyri, and occipital gyri.

The superior medial gyrus cluster was over 5 times more likely to fall within the semantic network and 12 times more likely to fall within the social network.

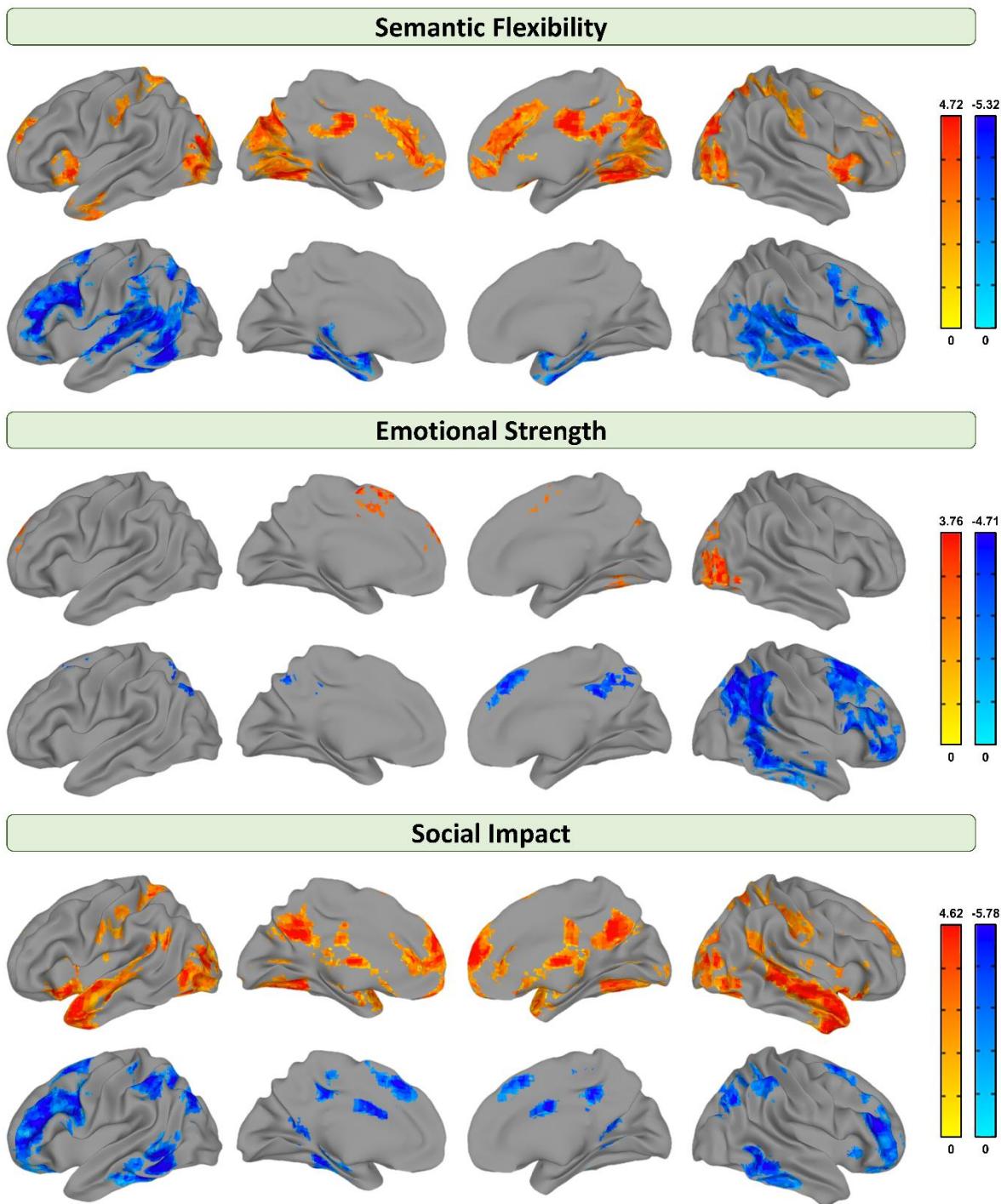
Decreases in Emotional Strength were associated with largely right lateralized activation in inferior, middle, and superior frontal gyri, inferior and middle temporal gyrus extending into inferior parietal lobule, and precuneus. One cluster (left inferior and superior parietal lobule and angular gyrus) overlapped with the semantic network (likelihood ratio: 9.66), but none of the remaining regions had substantial overlap with the semantic, social, or semantic control networks.

### 3.2.3 Social Impact

An increase in social, emotionally arousing words (indicated with positive Social Impact scores) was associated with activation in superior medial and frontal gyri, bilateral anterior temporal lobes extending posteriorly into middle and superior temporal gyri, bilateral inferior parietal lobule, anterior cingulate cortex, precuneus, and cerebellum. The largest cluster (peak voxel in right precuneus) captured portions of the semantic and social networks (likelihood ratios: 2.28 and 2.21, respectively). This extensive cluster included large portions of both left and right hemisphere temporal regions, and had high overlap with the semantic and social networks, but the ratios were moderate because this cluster also included many non-network voxels. The remaining cluster (superior medial gyrus and anterior cingulate cortex) had significant overlap with the social network (likelihood ratio: 9.04).

An increase in less social or emotionally arousing language (indicated with negative Social Impact scores) was associated with activation in inferior, middle, and superior frontal gyri, anterior and middle cingulate cortex, bilateral portions of superior parietal lobule, bilateral portions of inferior and superior temporal and fusiform gyri, and middle occipital gyri. There was minimal evidence of social network engagement to process this content (max likelihood ratio: 1.34). Clusters with peak voxels in left middle occipital gyrus (containing left inferior and superior parietal lobule and angular gyrus) and left inferior temporal gyrus (containing right superior parietal lobule and angular gyrus) overlapped with the semantic network (likelihood ratios: 3.56 and 8.29, respectively). The latter cluster also indicated

engagement of the control network (likelihood ratio: 6.13), which was also seen in the largest cluster containing left inferior frontal gyrus (likelihood ratio: 16.90).



**Figure 4. Semantic Flexibility, Emotional Strength, and Social Impact Results.**

The Z-score statistical maps are shown for each result with the range of values indicated by the associated colour bars. Warm colours (yellow to red) indicate regions with a positive correlation with the score, and cold colours (cyan to dark blue) indicate regions with a negative correlation with the score.

**Table 2***Cluster information*

Variable	Cluster Size	Hem	Brain Regions	% Overlap	MNI Coordinates			Semantic Network	Social Network	Control Network
					X	Y	Z			
Word Length	<b>4792</b>	L	<b>Inferior Frontal Gyrus (Triangularis)</b>	<b>32.2</b>	-38	30	21	<b>3.26</b>	<b>2.68</b>	<b>24.31</b>
Positive	4456	L	Inferior Frontal Gyrus (Orbitalis)	16.4						
		L	Precentral Gyrus	10.8						
		L	Inferior Frontal Gyrus (Opercularis)	8.6						
		L	Middle Frontal Gyrus	8.2						
		L	Temporal Pole	6.2						
	2821	R	<b>Medial Temporal Pole</b>	<b>6.1</b>	53	7	-23	1.94	<b>6.42</b>	<b>2.54</b>
		R	Inferior Frontal Gyrus (Triangularis)	26.1						
		R	Inferior Frontal Gyrus (Orbitalis)	16.0						
		R	Inferior Frontal Gyrus (Opercularis)	13.9						
		R	Precentral Gyrus	9.7						
Negative	2405	R	<b>Middle Temporal Gyrus</b>	<b>44.3</b>	53	-16	-10	<b>2.40</b>	<b>3.71</b>	-
		R	Superior Temporal Gyrus	35.8						
		R	Supramarginal Gyrus	5.7						
		R	<b>Supplementary Motor Area</b>	<b>26.5</b>	8	13	68	1.55	<b>6.64</b>	<b>6.28</b>
		R	Superior Medial Gyrus	25.6						
	560	L	Supplementary Motor Area	24.0						
		L	Superior Medial Gyrus	14.8						
		L	<b>Inferior Temporal Gyrus</b>	<b>63.3</b>	-53	-53	-20	<b>8.20</b>	-	<b>14.19</b>
		L	Middle Temporal Gyrus	25.2						
		R	<b>Posterior Cingulate Cortex</b>	<b>2.2</b>	2	-49	28	-	1.09	-
Word Length	10596	R	Precuneus	15.2						
		R	Superior Parietal Lobule	9.4						

		R	Middle Cingulate Cortex	6.4						
		R	Inferior Parietal Lobule	6.2						
		R	Angular Gyrus	5.4						
	6773	<b>L</b>	<b>Heschls Gyrus</b>	<b>3.0</b>	-40	-23	12	1.31	0.02	-
		L	Superior Temporal Gyrus	17.0						
		L	Postcentral Gyrus	16.8						
		L	Rolandic Operculum	9.6						
		L	Insula Lobe	5.9						
	5265	<b>R</b>	<b>Superior Temporal Gyrus</b>	<b>15.3</b>	53	-12	2	0.65	-	0.01
		R	Supramarginal Gyrus	9.5						
		R	Rolandic Operculum	9.5						
		R	Fusiform Gyrus	9.2						
		R	Insula Lobe	8.7						
		R	Postcentral Gyrus	5.3						
Number of Words <i>Positive</i>	9483	<b>L</b>	<b>Rolandic Operculum</b>	<b>3.1</b>	-40	-27	12	<b>11.85</b>	<b>3.86</b>	0.87
		L	Middle Temporal Gyrus	30.2						
		L	Superior Temporal Gyrus	11.7						
		L	Angular Gyrus	10.2						
		L	Inferior Temporal Gyrus	8.0						
	4870	<b>L</b>	<b>Superior Frontal Gyrus</b>	<b>24.4</b>	-10	26	64	<b>2.98</b>	<b>7.42</b>	0.37
		L	Middle Frontal Gyrus	24.6						
		L	Superior Medial Gyrus	23.8						
		R	Superior Frontal Gyrus	8.4						
		R	Superior Medial Gyrus	5.5						
		L	Supplementary Motor Area	5.0						
	3551	<b>R</b>	<b>Heschls Gyrus</b>	<b>6.1</b>	51	-15	6	<b>3.00</b>	<b>3.55</b>	-
		R	Superior Temporal Gyrus	30.2						
		R	Middle Temporal Gyrus	18.5						
		R	Inferior Temporal Gyrus	16.1						
		R	Medial Temporal Gyrus	11.4						
		R	Rolandic Operculum	5.2						
		R	Insula Lobe	5.1						
	1775	<b>L</b>	<b>Precuneus</b>	<b>45.3</b>	0	-60	36	-	<b>12.75</b>	-
		R	Precuneus	15.9						
		L	Posterior Cingulate Cortex	12.0						

		L	Middle Cingulate Cortex	7.5						
		R	Posterior Cingulate Cortex	5.9						
641		<b>R</b>	<b>Cerebellum (Crus II)</b>	<b>46.0</b>	20	-79	-40	-	<b>3.53</b>	-
		R	Cerebellum (Crus I)	37.0						
		R	Cerebellum (VI)	13.8						
587		<b>R</b>	<b>Angular Gyrus</b>	<b>86.1</b>	51	-61	27	-	<b>6.10</b>	-
138		<b>R</b>	<b>Cerebellum (IX)</b>	<b>45.3</b>	4	-55	-53	-	-	-
		L	Cerebellum (IX)	21.3						
			Cerebellar Vermis (IX)	16.6						
		L	Cerebellum (VIII)	6.5						
		R	Cerebellum (VIII)	6.5						
Number of Words	<b>63769</b>	L	<b>Insula Lobe</b>	<b>2.1</b>	-32	25	3	0.62	0.50	<b>2.66</b>
<i>Negative</i>										
Content Words	<b>14739</b>	R	<b>Inferior Frontal Gyrus (Triangularis)</b>	<b>6.4</b>	48	38	26	0.86	0.70	<b>8.76</b>
<i>Positive</i>		R	Middle Frontal Gyrus	18.4						
		L	Middle Frontal Gyrus	14.2						
		L	Inferior Frontal Gyrus (Triangularis)	9.7						
		R	Superior Frontal Gyrus	5.1						
10422		<b>L</b>	<b>Inferior Temporal Gyrus</b>	<b>14.8</b>	-55	-49	-20	<b>3.74</b>	0.21	1.80
		R	Inferior Temporal Gyrus	13.1						
		L	Fusiform Gyrus	8.3						
		R	Fusiform Gyrus	7.8						
		L	Middle Temporal Gyrus	7.7						
		R	Middle Temporal Gyrus	6.0						
		R	Parahippocampal Gyrus	5.9						
6243		<b>L</b>	<b>Heschls Gyrus</b>	<b>3.3</b>	-40	-23	12	<b>2.67</b>	0.17	-
		L	Inferior Parietal Lobule	24.1						
		L	Superior Temporal Gyrus	20.5						
		L	Middle Occipital Gyrus	8.8						
		L	Rolandic Operculum	6.0						
		L	Angular Gyrus	5.7						
5637		<b>R</b>	<b>Heschls Gyrus</b>	<b>3.8</b>	42	-21	8	0.60	0.19	-
		R	Superior Temporal Gyrus	16.8						

		R	Inferior Parietal Lobule	16.0						
		R	Angular Gyrus	13.7						
		R	Supramarginal Gyrus	10.1						
		R	Middle Occipital Gyrus	6.4						
		R	Insula Lobe	5.8						
		R	Superior Parietal Lobule	5.6						
1233		<b>L</b>	<b>Middle Cingulate Cortex</b>	<b>36.6</b>	-2	-37	42	-	0.03	-
		R	Middle Cingulate Cortex	40.5						
		L	Paracentral Lobule	5.9						
269		<b>L</b>	<b>Middle Cingulate Cortex</b>	<b>9.0</b>	-6	-1	30	-	-	-
		R	Middle Cingulate Cortex	18.1						
		L	Anterior Cingulate Cortex	18.0						
		R	Anterior Cingulate Cortex	5.6						
Content Words Negative	10101	R	<b>Precuneus</b>	<b>6.7</b>	6	-55	32	-	<b>2.39</b>	-
		R	Middle Occipital Gyrus	8.1						
		L	Precuneus	7.8						
		R	Lingual Gyrus	7.2						
		R	Fusiform Gyrus	6.8						
		R	Inferior Occipital Gyrus	5.8						
		R	Superior Occipital Gyrus	5.8						
5616		<b>L</b>	<b>Cerebellum (Crus II)</b>	<b>5.4</b>	-24	-78	-47	0.24	0.35	0.09
		L	Middle Occipital Gyrus	27.4						
		L	Lingual Gyrus	12.5						
		L	Inferior Occipital Gyrus	11.9						
		L	Fusiform Gyrus	11.0						
		L	Cerebellum (Crus I)	6.0						
		L	Superior Occipital Gyrus	5.8						
5208		<b>L</b>	<b>Supplementary Motor Area</b>	<b>6.3</b>	-8	19	68	1.97	<b>12.13</b>	0.34
		L	Superior Medial Gyrus	27.1						
		R	Superior Medial Gyrus	18.1						
		L	Superior Frontal Gyrus	16.8						
		R	Superior Frontal Gyrus	7.3						
		R	Supplementary Motor Area	6.5						
4235		<b>L</b>	<b>Inferior Temporal Gyrus</b>	<b>13.1</b>	-48	4	-45	<b>8.60</b>	<b>6.93</b>	<b>5.63</b>
		L	Middle Temporal Gyrus	23.1						

		L	Temporal Pole	14.3						
		L	Medial Temporal Pole	11.1						
		L	Inferior Frontal Gyrus (Orbitalis)	10.8						
2688		R	<b>Medial Temporal Pole</b>	<b>24.9</b>	53	9	-28	<b>4.04</b>	<b>5.53</b>	0.65
		R	Inferior Temporal Gyrus	21.5						
		R	Temporal Pole	18.8						
		R	Middle Temporal Gyrus	9.5						
		R	Inferior Frontal Gyrus (Orbitalis)	10.8						
		R	Insula Lobe	5.1						
1063		R	<b>Middle Temporal Gyrus</b>	<b>43.6</b>	48	-26	-11	<b>5.53</b>	<b>7.95</b>	-
		R	Superior Temporal Gyrus	30.6						
613		L	<b>Middle Temporal Gyrus</b>	<b>18.4</b>	-57	-55	23	<b>9.39</b>	<b>13.03</b>	-
		L	Angular Gyrus	38.3						
		L	Supramarginal Gyrus	23.3						
		L	Superior Temporal Gyrus	9.6						
253		R	<b>Cerebellum (Crus II)</b>	<b>47.1</b>	24	-81	-48	-	<b>7.18</b>	-
		R	Cerebellum (Crus I)	52.0						
Semantic Flexibility	37342	L	<b>Middle Occipital Gyrus</b>	<b>3.9</b>	-30	-79	15	0.06	0.38	0.25
Positive	785	L	<b>Inferior Temporal Gyrus</b>	<b>47.3</b>	-55	-2	-43	<b>4.40</b>	<b>3.36</b>	-
		L	Middle Temporal Gyrus	26.3						
Semantic Flexibility	13528	L	<b>Fusiform Gyrus</b>	<b>7.6</b>	-46	-53	-22	<b>9.28</b>	0.85	<b>2.01</b>
Negative		L	Middle Temporal Gyrus	15.8						
		L	Superior Temporal Gyrus	14.6						
		L	Inferior Temporal Gyrus	11.7						
		L	Inferior Parietal Lobule	7.5						
9160		R	<b>Heschls Gyrus</b>	<b>2.0</b>	40	-23	7	1.92	0.98	-
		R	Superior Temporal Gyrus	26.1						
		R	Middle Temporal Gyrus	20.9						
		R	Fusiform Gyrus	10.6						
		R	Inferior Temporal Gyrus	10.4						
4192		L	<b>Precentral Gyrus</b>	<b>16.5</b>	-42	7	31	<b>2.48</b>	1.33	<b>24.16</b>
		L	Inferior Frontal Gyrus (Triangularis)	39.5						
		L	Inferior Frontal Gyrus (Opercularis)	11.5						

		L	Middle Frontal Gyrus	11.0							
		L	Inferior Frontal Gyrus (Orbitalis)	8.8							
2726		R	<b>Inferior Frontal Gyrus (Triangularis)</b>	<b>47.1</b>	51	30	15	-	<b>3.64</b>	<b>3.97</b>	
		R	Inferior Frontal Gyrus (Opercularis)	17.6							
		R	Middle Frontal Gyrus	12.6							
		R	Precentral Gyrus	7.6							
764		L	<b>Middle Frontal Gyrus</b>	<b>64.9</b>	-24	6	57	-	-	-	-
		L	Superior Frontal Gyrus	30.8							
175		L	<b>Cerebellum (Crus II)</b>	<b>64.9</b>	-12	-81	-43	-	-	-	-
		L	Cerebellum (Crus I)	23.7							
153		R	<b>Inferior Frontal Gyrus (Orbitalis)</b>	<b>77.7</b>	32	34	-15	-	-	<b>3.46</b>	
		R	Middle Orbital Gyrus	12.8							
		R	Superior Orbital Gyrus	6.0							
Emotional Strength <i>Positive</i>	2377	R	<b>Inferior Occipital Gyrus</b>	<b>14.9</b>	42	-78	-14	-	0.11	-	
		R	Middle Occipital Gyrus	21.9							
		R	Superior Occipital Gyrus	11.3							
		R	Fusiform Gyrus	10.0							
		R	Lingual Gyrus	6.0							
		R	Inferior Temporal Gyrus	6.0							
1626		L	<b>Superior Medial Gyrus</b>	<b>27.9</b>	-6	58	34	<b>5.51</b>	<b>12.01</b>	1.72	
		L	Supplementary Motor Area	29.8							
		L	Superior Frontal Gyrus	24.6							
		L	Middle Cingulate Cortex	5.2							
Emotional Strength <i>Negative</i>	7414	R	<b>Middle Frontal Gyrus</b>	<b>29.9</b>	36	6	55	0.15	1.35	1.91	
		R	Inferior Frontal Gyrus (Triangularis)	15.7							
		R	Superior Frontal Gyrus	15.3							
		R	Inferior Frontal Gyrus (Opercularis)	10.8							
		R	Inferior Frontal Gyrus (Orbitalis)	6.9							
	6895	R	<b>Middle Temporal Gyrus</b>	<b>28.4</b>	53	-55	21	0.35	1.39	-	
		R	Angular Gyrus	20.0							

		R	Inferior Parietal Lobule	13.2							
		R	Inferior Temporal Gyrus	9.8							
		R	Supramarginal Gyrus	6.9							
		R	Superior Temporal Gyrus	5.2							
	659	<b>R</b>	<b>Precuneus</b>	<b>46.3</b>	6	-56	45	-	0.67	-	-
		R	Middle Cingulate Cortex	25.9							
		L	Precuneus	21.2							
		L	Middle Cingulate Cortex	5.4							
	402	<b>L</b>	<b>Middle Occipital Gyrus</b>	<b>20.1</b>	-40	-76	33	<b>9.66</b>	-	-	-
		L	Inferior Parietal Lobule	36.0							
		L	Angular Gyrus	33.8							
		L	Superior Parietal Lobule	7.0							
	370	<b>L</b>	<b>Middle Frontal Gyrus</b>	<b>82.2</b>	-26	7	61	-	-	-	-
		L	Superior Frontal Gyrus	14.8							
Social Impact	48193	<b>R</b>	<b>Precuneus</b>	<b>2.0</b>	2	-55	28	<b>2.28</b>	<b>2.21</b>	0.20	
	6986	<b>L</b>	<b>Superior Medial Gyrus</b>	<b>20.8</b>	2	57	18	0.75	<b>9.04</b>	-	
		R	Superior Medial Gyrus	19.0							
		R	Superior Frontal Gyrus	11.6							
		L	Anterior Cingulate Cortex	9.4							
		R	Anterior Cingulate Cortex	7.2							
Social Impact	8909	<b>L</b>	<b>Inferior Frontal Gyrus (Triangularis)</b>	<b>16.4</b>	-38	30	21	1.55	1.34	<b>16.90</b>	
Negative		L	Middle Frontal Gyrus	24.9							
		L	Precentral Gyrus	8.6							
		L	Superior Frontal Gyrus	8.3							
		L	Inferior Frontal Gyrus (Opercularis)	6.6							
		L	Inferior Frontal Gyrus (Orbitalis)	6.2							
		L	Middle Orbital Gyrus	5.1							
	4935	<b>R</b>	<b>Inferior Frontal Gyrus (Triangularis)</b>	<b>16.5</b>	46	36	17	-	0.26	1.96	
		R	Middle Frontal Gyrus	41.9							
		R	Middle Orbital Gyrus	10.4							
		R	Inferior Frontal Gyrus (Orbitalis)	10.2							
		R	Superior Frontal Gyrus	9.5							

		L	<b>Middle Occipital Gyrus</b>	<b>15.5</b>	-40	-78	33	<b>3.56</b>	0.20	-
		L	Inferior Parietal Lobule	45.9						
		L	Angular Gyrus	10.9						
		L	Superior Parietal Lobule	6.5						
3618		L	<b>Inferior Temporal Gyrus</b>	<b>39.1</b>	-59	-49	-15	<b>8.29</b>	0.17	<b>6.13</b>
		L	Middle Temporal Gyrus	31.0						
		L	Fusiform Gyrus	14.1						
3398		R	<b>Inferior Parietal Lobule</b>	<b>30.9</b>	48	-46	52	-	0.01	-
		R	Angular Gyrus	24.3						
		R	Supramarginal Gyrus	14.5						
		R	Middle Occipital Gyrus	12.3						
2500		R	Superior Parietal Lobule	6.1						
		R	<b>Middle Temporal Gyrus</b>	<b>30.2</b>	63	-49	-8	-	-	-
		R	Inferior Temporal Gyrus	66.8						
1481		R	<b>Middle Cingulate Cortex</b>	<b>32.0</b>	2	-39	41	-	-	-
		L	Middle Cingulate Cortex	47.1						
915		L	Paracentral Lobule	7.7						
		L	<b>Anterior Cingulate Cortex</b>	<b>18.4</b>	-2	-1	30	-	-	-
		L	Middle Cingulate Cortex	13.8						
390		R	Middle Cingulate Cortex	12.7						
		R	Anterior Cingulate Cortex	5.7						
291		R	<b>Calcarine Gyrus</b>	<b>10.1</b>	14	-54	12	-	-	-
		R	Precuneus	50.5						
		R	Lingual Gyrus	25.2						
			Cerebellar Vermis (IV/V)	5.8						
271		L	<b>Calcarine Gyrus</b>	<b>28.7</b>	-8	-52	4	-	-	-
		L	Precuneus	46.2						
		L	Lingual Gyrus	8.3						
		L	Cuneus	6.7						

Note. Hem, Hemisphere; L, Left; R, Right. Cluster size is determined by the number of 2mm<sup>3</sup> voxels. % Overlap is the percent overlap between each cluster and the atlas defined regions (based on the Eickhoff-Zilles macro labels from the N27 (MNI space) atlas). The regions which contained the peak voxels are bolded. MNI coordinates correspond to the voxel with peak activation within each cluster. Voxels were defined as neighbours based on faces touching (NN=1). The last three columns report the

likelihood ratios for the semantic, social, or semantic control network. Ratios indicating that the voxels within the cluster are 2 or more times more likely to belong to the network than voxels outside the cluster are bolded. Percent overlap values are presented in a supplementary table on OSF (<https://osf.io/u54dr/>).

### *3.3 The roles of the semantic, social, and semantic control networks*

The likelihood ratio was calculated separately for each brain network overlapped with the full results of the content words, Semantic Flexibility, and Social Impact analyses using the formula described previously. The resulting ratio provides an estimate of overlap relative to non-overlap between the full result and each network. Those values are presented in **Figure 5**.

#### **3.3.1 Semantic cognition network**

As expected, the positive content words result indicated engagement of parts of the semantic network (likelihood ratio: 2.04). The overlap was predominately in portions of left inferior parietal, left inferior frontal, left inferior temporal, and bilateral superior temporal regions. The negative content words result, however, also indicated engagement of a substantial portion of the semantic network (likelihood ratio: 2.67)<sup>2</sup>. The negative content words result overlapped with the semantic network in bilateral anterior temporal, middle and superior temporal, and left supramarginal gyri, which was unanticipated given the role of these regions – particularly the anterior temporal lobes (Lambon Ralph et al., 2017) – in processing semantic content.

The negative Semantic Flexibility result, capturing increased infrequent, less semantically diverse language, substantially overlapped with the semantic network (likelihood ratio: 6.16); indeed, this result aligned with the semantic network more than any of the other results. The overlap predominately occurred in the left fusiform gyrus, bilateral superior temporal and left frontal regions (orbital portion of the inferior frontal gyrus and precentral gyrus). The positive Semantic Flexibility result, which reflected more frequent, semantically diverse language, tended to fall outside of the semantic network (likelihood ratio: 0.14), except for a small portion of left anterior inferior temporal lobe.

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<sup>2</sup> The likelihood ratio was also slightly higher, suggesting that there was more overlap between the network and this result than the positive content words result. It is important to note that the positive content words result included a larger network of regions than the negative content words result, so the reduced ratio indicates that the result included more regions *outside* of the semantic network.

Both the positive and negative Social Impact results included large portions of the semantic network (likelihood ratios: 2.11 and 2.19, respectively). These results suggest that regions within the semantic network - as well as regions outside of the network - were modulated by socially and emotionally arousing language. The overlap between the semantic network and the positive Social Impact result occurred within the bilateral anterior temporal lobe, left inferior parietal lobule, left superior medial frontal gyrus, left inferior frontal gyrus, and left hippocampus. The overlap between the semantic network and the negative Social Impact result occurred in left frontal regions (precentral gyrus, inferior frontal gyrus, superior medial gyrus), temporal regions (bilateral superior temporal gyrus, left inferior temporal, left fusiform), and in a posterior portion of the left angular gyrus.

In summary, different regions within the semantic cognition network were engaged by increased and decreased semantic or social content. Perhaps most notably, ATL subregions showed differential sensitivity to fluctuations in content words. As the number of content words increased, so did activation in the ventral portion of ventrolateral ATL in anterior inferior temporal gyrus and fusiform gyrus, consistent with the role of this region as a transmodal hub of semantic processing (Lambon Ralph et al., 2017). As the number of content words decreased, the temporal pole and anterior middle and superior temporal portions of ATL were engaged, alongside regions within the default mode network. A similar network of regions, including these latter ATL subregions, was engaged when there was *more* social content. Presentation of highly frequent, semantically diverse language appeared to disengage the semantic network outside of a portion of left ATL.

### 3.3.2 Social cognition network

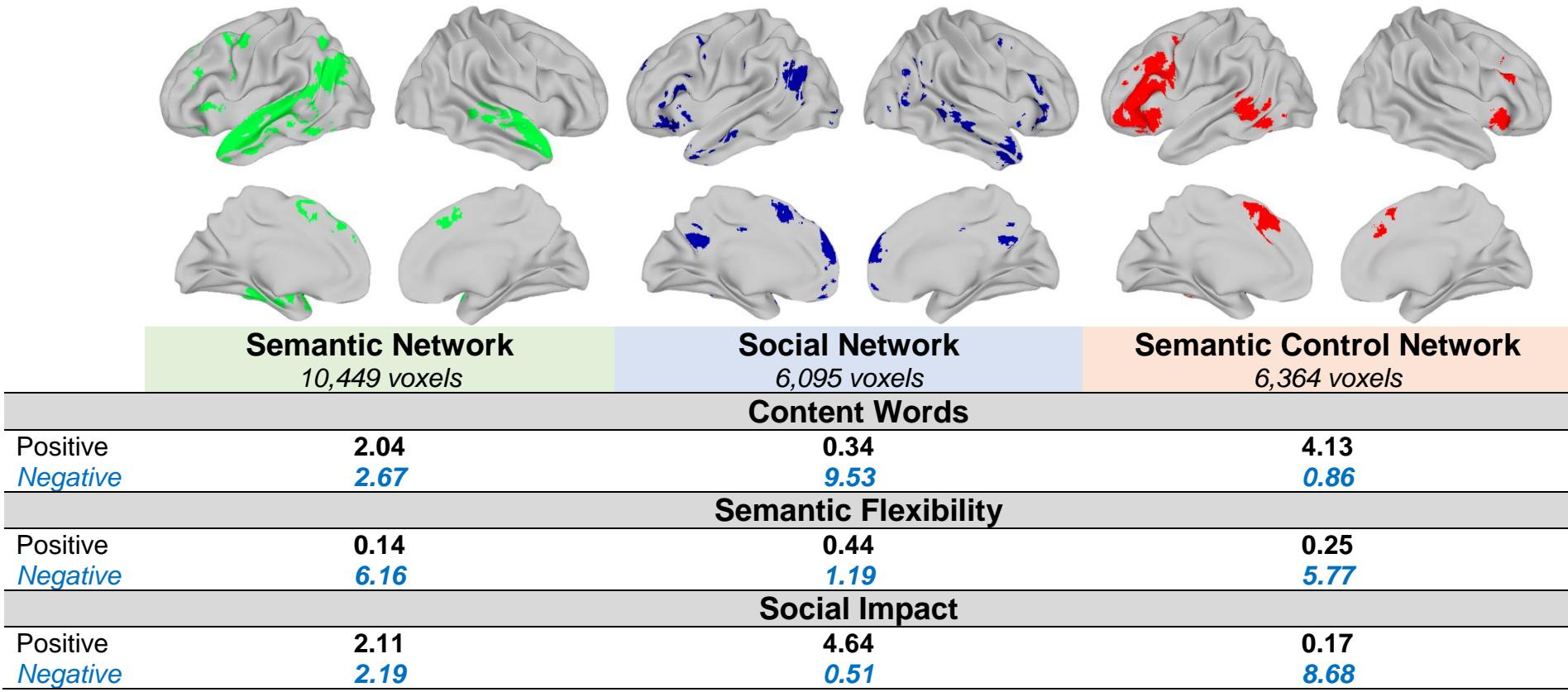
The positive Social Impact result, which identified regions that were modulated by more social and emotionally arousing language, captured a large portion of the social cognition network. The voxels that were modulated by more social and emotionally arousing language were over 4 times more likely to fall within the social cognition network than voxels that were not modulated by positive Social Impact. The overlap occurred in bilateral anterior temporal and middle temporal (predominately right hemisphere) regions, the orbital part of inferior frontal gyrus,

and supramarginal gyrus. The social network was not meaningfully engaged when there was reduced social and emotionally arousing language (likelihood ratio: 0.51).

Neither increased Semantic Flexibility nor an increase in content words modulated regions within the social network; however, a decrease in content words engaged a substantial portion of the social network (likelihood ratio: 9.53). This reflects the similarity in the networks captured by reduced content words and increased Social Impact.

### 3.3.3 Semantic control network

The semantic control network did not appear to be recruited when word-level Semantic Flexibility increased, and instead was recruited when Semantic Flexibility decreased. The likelihood ratios indicated that voxels within the positive Semantic Flexibility result were more likely to fall *outside* the semantic control network than within it (0.25), whereas the negative Semantic Flexibility result voxels were more than 5 times more likely to fall *within* the semantic control network (5.77). The negative Semantic Flexibility result captured a large portion of the control network, particularly in bilateral inferior frontal gyri (predominately left hemisphere) and posterior inferior and middle temporal gyri. Overlap in these regions was also observed for the increased content words and, to an even greater extent, the decreased Social Impact results (likelihood ratios: 4.13 and 8.68, respectively).



**Figure 5. Engagement of the semantic, social, and semantic control networks.** The semantic network (green), social network (blue), and semantic control network (red) derived from meta-analytic studies are shown at the top of the figure. The likelihood ratio is shown for each result. Values greater than 1 indicate an increased likelihood of belonging to the network compared to falling outside the network. These values are reported for the increased (positive) and decreased (negative) content words (first row), Semantic Flexibility (second row), and Social Impact (third row) results.

## 4 Discussion

Two accounts make seemingly conflicting claims about the organization of the semantic system: semantic processing is said to rely on a multimodal hub architecture (hub-and-spoke framework) or said to display voxel-wise category specialization across a large, distributed network (semantic tile framework). Reconciling these claims is complicated by them being derived from very different kinds of data. The hub-and-spoke framework is primarily based on well-controlled studies of the lexical and semantic properties of isolated words or sentences, whereas the semantic tile framework is based on studies using different approximations of word-level representations in natural language or narratives. The aim of the present study was to reduce the theoretical and methodological disparities between these two approaches by investigating how lexical and semantic variables, akin to those that informed the hub-and-spoke model, are processed in a narrative. In doing so, we can use prior studies of isolated words to make predictions about brain regions that will respond to these semantic variables and compare the networks observed with prior naturalistic work, thus moving toward an integrated account of semantic cognition.

Our results suggest that, in contrast to studies of isolated word processing, large networks are engaged by and are differentially sensitive to lexical-semantic content in narratives. These large networks have considerable overlap with the semantic, semantic control, and social cognition networks and often include portions of two or more of these known networks, suggesting some degree of shared resources for processing different types of lexical-semantic information in more realistic contexts. Studies using single words, sentences, or short passages typically identify relatively small regions that respond to particular lexical or semantic properties (e.g., Bucur & Papagno, 2021; Graves et al., 2010; Hauk et al., 2008); even the “language network” recently identified in a large-scale study is substantially narrower than the patterns we report here (Malik-Moraleda et al., 2022). Considering that the present study used an auditory language comprehension task – and the language was not particularly difficult (*The Little Prince* is considered middle-grade literature, appropriate for children ages 11–14) – it is notable that the results were so broadly distributed, typically across multiple networks. This aligns with prior research examining narrative comprehension, which found overlapping, bilateral networks,

rather than isolated regions, to be selective for semantic categories (Zhang et al., 2020). The sections that follow provide discussion of the whole-brain exploratory analyses in comparison to prior single-word studies and, where relevant, the corresponding hypothesis-driven analyses of network behaviour. We conclude with a discussion of limitations on the inferences that can be made from this study and implications for the neural basis of language comprehension and future research.

#### **4.1 General lexical and semantic content**

The first set of analyses examined neural correlates of the general lexical or semantic content quantified using three complementary measures: number of words, number of content (open class) words, and the Word Length factor. Unsurprisingly, the semantic network was engaged when a time window contained more words. The particular regions included the superior temporal gyri, which are routinely reported to be engaged during narrative comprehension (Alho et al., 2006; Crinion et al., 2003; Wilson et al., 2008), and the left angular gyrus, which is in both the semantic and social cognition networks and is involved in combinatorial processing during narrative comprehension (Baldassano et al., 2017; Lahnakoski et al., 2017; Stephens et al., 2013) and in speech comprehension more generally (Crinion et al., 2003; Wilson et al., 2008). These results also converge with networks observed in studies of psycholinguistic properties (including word quantity) in briefer passages of speech (50-60 seconds) (Awad et al., 2007; Wu et al., 2022), suggesting some stability in network engagement across the duration of narratives.

Although there was extensive overlap between the networks responsive to number of words and number of content words, the activity dissociated in two key regions: bilateral anterior temporal lobes and left inferior parietal lobule. Activity in ventral ATL, a portion of the transmodal ATL semantic hub, was associated with an increase in content words only, and was not engaged by a general increase in quantity of words. Activity in the rest of the ATL and the IPL was associated with decreases in number of content words and increases in overall quantity of words.

Decreases in number of words were associated with increased activation in the default mode network (DMN) (Raichle, 2015), including frontal, cingulate, and posterior temporal and parietal regions, which may reflect self-generated internal

processing of the narrative (Andrews-Hanna et al., 2014; Buckner & Carroll, 2007). A different network of regions co-varied with a decrease in content words, most notably the temporal pole and middle temporal portion of ATL. Prior research has found that these ATL subregions and regions within the DMN accrue information over longer timescales and for coherent stories (Simony et al., 2016) – a distinctive property of narratives. Time windows with fewer words may decrease the demands of processing incoming language input, allowing for reflective, integrative processing and reasoning about the events in the narrative, which engages these default mode regions. Narrative moments with less semantic content may similarly provide the reader with an opportunity to reflect on the events and incorporate local information with the global context. These moments appear to be supported by a portion of ATL, predominately lateral temporal pole, whereas ventral ATL is engaged in processing narrative moments with more word-level semantic content.

**Network Behaviour.** As expected, the semantic and the semantic control systems were engaged as the number of content words increased. Surprisingly, approximately equally large areas of the semantic network responded to increases and to decreases in number of content words. A portion of the transmodal hub in ventrolateral ATL was selective for semantic content: a general increase in words did not engage the hub, but an increase in *content* words did. Interestingly, other ATL subregions, including temporal pole and middle and superior temporal gyri, were engaged during time windows with fewer content words.

This counterintuitive recruitment of semantic brain regions when there are fewer content words may reflect the complex relationship between overall word quantity, content word quantity, and semantic processing demands in a narrative context. Importantly, a decrease in the amount of content words does not always indicate that fewer total words were being processed: the number of words and the number of content words were only moderately correlated ( $r = 0.45$ ), and the number of content words could only ever be equal to or less than the number of words. The constraints of audiobooks and story-telling mean a relatively consistent speech rate and narrative progress to keep the listener engaged. For example, the excerpt “*...I am precise and what do you do with these stars what do I do with them...*” includes only 2 content words (precise, stars) but has a total of 17 words. For comparison,

consider the excerpt “...we write about eternal things but extinct volcanoes can wake...”, in which 7 of the 10 words are content words.

We speculate that, during narrative comprehension, there is a division of labour within the semantic cognition system, in particular within ATL, that facilitates the mapping of individual word meanings and combinatorial processing. As the amount of semantic content increases, a portion of the transmodal hub in ventral ATL is selectively engaged to access content word meanings, consistent with prior accounts of the graded contributions of ATL (Lambon Ralph et al., 2017). When the relative amount of semantic content is reduced, the temporal pole and middle and superior temporal subregions are engaged. During these time windows, narrative information is nevertheless being conveyed and listeners may engage in more extensive integration of these semantically “light” words with narrative context. A period with little new semantic content may also provide an opportunity to reflect on recently-presented information and integrate this with the existing mental model of the narrative, which is consistent with the roles left angular gyrus and ATL play in semantic integration (Bonnici et al., 2016; Humphries et al., 2007; Kuhnke et al., 2022; Lambon Ralph et al., 2017). This interpretation is complemented by our finding that increases in number of content words were associated with increased activity in a large portion of the control network, specifically left inferior frontal and inferior and middle temporal regions. These control regions were not activated by increased overall number of words, so it may be that the control system is particularly important for integrating new word-level information (i.e., content words) into the situation model.

In summary, we expected activation of the semantic network to positively scale with an increase in content words, but word quantity may be an incomplete operationalization of semantic demand. Ventral ATL did exhibit the expected positive association, but the rest of the ATL, along with other key semantic regions, including the IPL hub, exhibited the opposite response pattern. The inverse narrative situation – when there are fewer content words – may give readers/listeners the chance to integrate the details with the narrative or facilitate a greater depth of processing of the concepts presented, which engages these portions of the semantic system. Considering that ATL and IPL are “semantic hubs” that are reliably activated during lexical-semantic processing (Binder & Desai, 2011; Jefferies et al., 2020), this is one

of several results from the present study that suggest caution in generalising the neural basis of semantic cognition from single-word to narrative comprehension. Despite the considerable insights generated about the neurobiology of the language system from single-word studies, these studies provide only a partial understanding of how the language system is engaged in real-world settings. A complementary approach in which single-word studies generate the hypotheses that subsequently constrain and guide naturalistic investigations may be ideally suited to maximize the advantages of both. The present study, however, underscores the potential pitfall in presuming that the brain regions observed in single-word studies behave in an analogous way in response to narrative or other naturalistic stimuli.

## 4.2 *Semantic dimensions*

Analogous whole-brain exploratory analyses were conducted with variables capturing different dimensions of semantic content, which were derived from a PCA of word-level lexical-semantic properties.

### 4.2.1 Semantic Flexibility

The Semantic Flexibility factor was most strongly driven by semantic diversity, which measures the contextual variation of words (Hoffman et al., 2013). Words with high semantic diversity occur in wide-ranging contexts compared to words with low semantic diversity, which occur in a more constrained set of similar contexts. Semantically diverse words tend to be more ambiguous, with varied context-dependant meanings. An increase in semantic diversity (and corresponding increase in positive Semantic Flexibility scores) was thus expected to require the same cognitive mechanisms and neural systems involved in resolving semantic ambiguity: bilateral anterior inferior temporal gyrus, middle temporal gyri, middle frontal regions, and, especially, bilateral inferior frontal gyrus (MacGregor et al., 2020; Rodd et al., 2010, 2012; Vitello & Rodd, 2015). The posterior temporal gyri are also commonly reported in studies of semantic ambiguity resolution, although the role of this region is less clear. In a study of homonym comprehension, posterior middle temporal gyrus was thought to act as an intermediary between the semantic and control systems (Hoffman & Tamm, 2020).

In the present study, increased activation in these regions was observed as Semantic Flexibility scores decreased. Decreased scores reflect more concrete, less frequent, and less semantically diverse words, which should produce easier meaning selection and are less likely to require the resolution of ambiguity. Superficially, this conflicts with the single-word and sentence semantic ambiguity literature. There are three potential reasons for this apparent discrepancy.

First, many studies of semantic ambiguity focus on homonyms (e.g., *bark*, *bank*), which have multiple specific meanings and - without context - it is unclear which meaning is being referenced (Hoffman & Tamm, 2020; Kadem et al., 2020). In the current analysis, words with the highest Semantic Flexibility scores were not homonyms; they were highly frequent, less concrete, very semantically diverse words that have highly context-specific meanings (e.g., *so* and *where*). In fact, the highly frequent homonyms that were present in the story ( $n = 58$ , based on frequency estimates from a prior study (Rice et al., 2019)), received much lower Semantic Flexibility scores ( $M = 0.08$ ) compared to non-homonyms ( $M = 0.39$ ). Thus, the Semantic Flexibility factor does not capture the need to select between alternative divergent meanings of a word, which is the type of lexical ambiguity that prior studies have typically investigated.

Second, even if the Semantic Flexibility factor did capture ambiguity as defined in previous studies, context helps to resolve homonym-type ambiguity by priming the correct meaning, as many studies have shown (e.g., Binder & Morris, 1996; Blott et al., 2022). This kind of context is always present in narratives, so the priming provided by a coherent narrative provides an informed and rapid route to select the appropriate word meaning and navigate ambiguities with relative ease. That is, when homonyms occur in natural narratives, their meanings are usually not ambiguous because of the extensive context.

Third, research on semantic ambiguity typically compares processing of ambiguous words with carefully matched (i.e., equally frequent, concrete, short, etc.) non-ambiguous words or sentences. In natural language, these variables are not orthogonal, so ambiguous words tend to vary along other dimensions as well. The lowest Semantic Flexibility scores, for instance, were given to words that have little ambiguity in meaning but also are low in frequency and have few semantic neighbours (e.g., *footstool* and *lamplighter*). These words are not ambiguous, but do

have complex and rarely-accessed meanings, which could place high demands on the semantic system. Thus, the neural effects are likely being driven in part by the other properties that load on the factor, such as frequency. For the Semantic Flexibility and Social Impact results, activation in left fusiform gyrus may be driven by an increase in concreteness, which inversely loaded on both of these factors (Bucur & Papagno, 2021; Hoffman et al., 2015; Wang et al., 2010). This difference between the Semantic Flexibility scores in this study and traditional experimental psycholinguistic manipulations reflects a trade-off between experimental control and ecological validity: comparing processing of homonyms with matched unambiguous words may isolate meaning selection processes, but these may be very different processes than ones involved in dealing with semantic ambiguity as it occurs in narrative contexts.

**Network Behaviour.** Increased Semantic Flexibility did not engage the semantic or semantic control systems. Instead, *decreased* Semantic Flexibility was associated with recruitment of large portions of both the semantic and control networks, as well as a small portion of the social network. As discussed above, this factor approximated semantic ambiguity but the context of a narrative and the use of semantic diversity made the words with high, positive scores quite different from traditional single-word or sentence-level ambiguity manipulations. The concepts that strongly, negatively loaded onto this factor were longer, infrequent words that placed additional demands on the semantic control system, which is evident in the high degree of control system engagement. Consider the example of a low Semantic Flexibility window provided in **Table 1**, the concepts “constrictors” and “primeval” are not ambiguous because they have only one meaning but they are also more difficult to process than the more frequent concepts in the high Semantic Flexibility example. The present results suggest that, during narrative comprehension, control systems in inferior frontal gyrus and posterior middle temporal gyrus are most strongly engaged when retrieving the meanings of unusual, low-frequency words (Jackson, 2021; Wu et al., 2022). The observed activation in left fusiform gyri and bilateral inferior frontal gyri may also be driven by the infrequency of the words (Carreiras et al., 2009; Hauk et al., 2008). It is thus likely, although perhaps counterintuitive, that control mechanisms were recruited to update situation models based on semantically heavy

words with lower Semantic Flexibility scores, rather than to disambiguate individual words.

#### 4.2.2 Emotional Strength

Emotion can be conceptualized as being comprised of at least two complementary dimensions: valence and arousal (Citron, 2012). Arousal, which loaded on the Social Impact factor, is thought to be more automated and to engage perceptual and physiological systems. The Emotional Strength factor most closely approximated emotional valence, which is thought to require an evaluative judgement that engages higher order cognitive systems and is less automated (Citron, 2012; Cunningham et al., 2004).

An increase in Emotional Strength engaged right inferior and superior occipital gyri, portions of right fusiform and inferior temporal gyri, left superior medial gyrus, and middle cingulate cortex. These results partially converge with a prior study which reported activation in right superior occipital gyrus in response to increased emotionality (irrespective of direction) in contrast to neutral words (Citron et al., 2014). Engagement of superior medial gyrus and middle cingulate is consistent with prior investigations of written word processing, although the anterior portion of the cingulate cortex is more consistently reported (Citron, 2012). Interestingly, decreased Emotional Strength was associated with activation in predominately right-lateralized regions. Prior research has isolated a similar network of regions that respond to the semantic category of *emotion* (Zhang et al., 2020). In the present study, these regions do appear to be modulated by emotion, but not in the expected direction.

Importantly, however, our Emotional Strength factor was transformed such that the anchor points on either end did not correspond to negative and positive emotional valence, and instead corresponded to the overall emotional extremity of the word, agnostic to valence direction. Although similar approaches have been taken in other neural investigations of valence (Citron et al., 2014; Cunningham et al., 2004), this may be an important deviation from prior research. For instance, there may be differences in how negatively and positively valenced words are processed, with negative words possibly being processed more deeply and slowly (Kuperman et

al., 2014). This valence asymmetry may alternatively be driven by higher semantic similarity for positive compared to negative information, which, in the case of the latter, might result in an increased processing cost (Alves et al., 2017; Meersmans et al., 2020). Prosodic information such as pitch was also not considered in the current analysis. These features are likely to correlate with the emotional features of a narrative, so it is possible that the results captured here include regions associated with prosodic processing, an essential component of real-world emotion processing, and not solely emotion information (although the results differ from an isolated analysis of pitch within this narrative (Li et al., 2022)). The pitch information is included as part of the dataset and is thus a viable direction for future research.

#### 4.2.3 Social Impact

Prior studies have consistently identified bilateral superior ATL, ventrolateral ATL, and occasionally prefrontal regions and posterior middle temporal regions in processing abstract, social concepts (Binney et al., 2016; Pobric et al., 2016; Zahn et al., 2007). In our study, the network engaged by increased social and emotionally arousing language did include bilateral ATL, but did not include the amygdala, which is commonly reported in studies of emotional arousal (Citron, 2012).

A recent theoretical account argues that social conceptual knowledge is a type of semantic memory, nested within the neural architecture of the semantic cognition system (Binney & Ramsey, 2020). Building upon this theoretical framework, the graded semantic hub hypothesis suggests that the ventrolateral ATL is a domain-general hub for processing varied semantic representations, including social knowledge, with graded shifts in functional specialization occurring proximal to this hub (Binney et al., 2016). This account is supported by recent evidence of activation in this ventrolateral subregion across three theory of mind tasks (using linguistic and non-linguistic stimuli) and a non-verbal semantic association task (Balgova et al., 2022). This suggests that social knowledge, including mental state inference, which theory of mind tasks probe, is at least partially processed within the semantic system, and this domain-general hub of the semantic system is centred on the ventrolateral aspect of left ATL. The present results are consistent with this account. Increases in more flexible or semantically diverse language (i.e., increased Semantic Flexibility) and increased Social Impact both engaged a portion of this ventrolateral

ATL region. Specialization for social conceptual knowledge appears to be present in the dorsolateral ATL, which was not observed for Semantic Flexibility and which converges with prior evidence of specialization in this part of ATL for processing abstract, social concepts (Zahn et al., 2007).

Increased Social Impact was associated with activity in a similar network of regions as decreased number of content words. These regions, which include bilateral ATL, middle temporal gyri, and IPL, are upregulated when the amount of semantic content was minimal or when the content was social. Importantly, the Social Impact scores were not correlated with the number of content words ( $r = -0.06$ ), so the analyses are not capturing the same underlying semantic information despite the similarity in the results. Recruitment of semantic hubs may suggest that in both cases the nature of the local passage places additional demands on the semantic system – either because there are few concepts presented so they are processed more deeply or because when several social concepts are presented rapidly they must be holistically integrated.

**Network Behaviour.** As expected, increases in social content recruited the social and semantic networks, but not the control network. Although the overlap with the control network was minimal, a small portion of anterior IFG co-varied with increased social content, which aligns with our predictions. The positive Social Impact result overlapped with the core hubs within semantic network, which may indicate that social, high-arousal words are a special type of semantic concept that engage the semantic system.

The social cognition network as defined here was derived from studies of much more abstract social processes, such as trait judgement and empathy for others or pain (Diveica et al., 2021). The fact that large portions of this network were also identified in the semantic network and were modulated by social concepts was predicted as a key piece of converging evidence that semantic memory may include aspects of social cognition and that these systems work cooperatively or integratively. Social concepts are a type of semantic knowledge and are consistently reported to engage superior/dorsolateral ATL (Binney et al., 2016; Pobric et al., 2016; Zahn et al., 2007), so hypothesizing the role of the semantic system in processing these concepts was strongly motivated by prior research. The involvement of the task-general social cognition system was less certain (Binney &

Ramsey, 2020) and suggests that retrieving the social meaning of words engages the broader social cognition network – a network that is defined by activation during abstract social tasks that rarely rely on isolated written or spoken language. Complex social reasoning is required for narratives, such as the story used here, which often involve rich descriptions of human interactions and social behaviours, and perhaps even oversample such scenarios for compelling story-telling.

A majority of the control network was recruited as Social Impact decreased, suggesting that social and emotionally arousing language did not require additional control mechanisms. Windows that received strongly negative Social Impact scores were those with more neutral, factual, or purely informative content. The example provided in **Table 1** illustrates this well: “*...as a tree falls there was not even any sound because of the sand...*”. The results suggest that the control network is recruited when complex information critical to narrative comprehension is presented in a short period of time and needs to be integrated quickly into the situation model.

The same ventrolateral portion of left ATL was engaged by increases in two of the dimensions of semantic content investigated here. A more ventral portion of ventrolateral ATL was engaged when general semantic content increased (number of open class words). This is in contrast to the *disengagement* of the temporal pole when semantic content decreased. This suggests that left ATL may not be uniformly engaged by all categories of concept and instead is selectively upregulated for processing different types and amounts of semantic information. This is consistent with prior work on the graded functioning of ATL (Lambon Ralph et al., 2017). The portion of this hub that was engaged by social content, for example, differed slightly from the portion engaged by semantic content more generally, possibly driven by proximity to the dorsolateral ATL region that may display specialization for social concepts (Balgova et al., 2022). Engagement of temporal pole during narrative moments with relatively fewer semantic concepts may reflect depth of semantic processing, which is also enhanced by an increase in social semantic content (Social Impact). These moments allow for deeper semantic integration with the preceding narrative context.

#### *4.3 Inferential considerations*

There are several considerations worth noting when generating inferences from the present study. First, the factor scores were only generated for open class words (i.e., content words). A similar approach has been adopted in other work examining word-level psycholinguistic properties during narrative comprehension and production (Wu et al., 2022). In addition, studies of single word or sentence level processing almost exclusively focus on open class words, and the aims of the current investigation were to study how those types of words are processed when presented in a rapid narrative context. Although closed class words were excluded from analysis, they certainly contribute to scaffolding understanding of an unfolding narrative.

Second, it is important to consider the narrative context in which concepts are likely to be used and their distribution across narrative contexts. Prior research has shown a high degree of correspondence between the emotional properties of the lexical units that comprise a sentence or brief narrative and subjective ratings of the emotion at the sentence and passage level (Bestgen, 1992; Hsu et al., 2015). This suggests that using word properties as a proxy for sentence and passage content is a viable starting point, at least for emotion-based concepts, but extending this to the narrative and discourse levels requires further validation. Narratives benefit from deep context and background, so it is possible for sentences or passages to have strong emotional or social impact without containing many intrinsically emotional or social words. It may be that emotional and social moments within a narrative do not require and maybe do not even heavily rely on emotional or social language. Although certainly possible, it is not clear how often this situation occurs outside of rare moments or particular literary styles.

Third, the meta-analytic network definitions were necessarily limited by the studies used as input for ALE analyses. These studies relied on contrast-based methods with predominately word or sentence stimuli. Defining networks, such as the semantic network, in this way is advantageous because it allows for a comparison of word-level processing in a narrative context against results from single word or sentence level studies. It does not fully capture an inclusive network definition that accounts for data from naturalistic paradigms. There is currently no standardized way to statistically aggregate the results of analyses (or even standard

analysis approaches) used in naturalistic neuroimaging studies. The network maps we used are therefore an approximation at best and are themselves generated without consideration for naturalistic narrative contexts.

## 5 Conclusion

The present study is a step toward extending theories of semantic cognition based on isolated stimuli to explaining semantic cognition in narrative contexts. Studies of isolated stimuli assume that words have meaning on their own and by presenting them individually and in random order, we can identify the regions that represent a lexical or semantic property. Further, there is an implicit presumption that the neural response will be additive when presented in naturalistic contexts: the same region(s) will be recruited to process words with a given property plus the regions needed to process the component parts of the naturalistic stimuli. This is not what we observed in the current study. Counter to expectations grounded in isolated-stimuli experiments, we observed that fluctuations in a single lexical or semantic property co-varied with activation in large brain networks. Further, *a priori* networks based on meta-analyses did not behave in a straightforward or uniform way: some network subregions were engaged more strongly by an increase in semantic content, while other subregions were engaged by a decrease. This is an important deviation from how the semantic, semantic control, and social networks are currently conceptualized. Prior, non-naturalistic studies used more simplified stimuli, which may have resulted in more focal results and the impression that small regions independently represent a larger, more complex cognitive system. We interpret these results as evidence that cognition is not additive in nature and instead cognitive systems jointly process complex stimuli. An implication of this view is that functional specialisation is a dynamic property and that networks do not have clear and consistent boundaries that allow them to act as additive components during cognitive processes such as language comprehension (Aguilera & Di Paolo, 2021; Behrmann & Plaut, 2013; Friston et al., 2021; Yeo et al., 2015).

The extent of the networks engaged here align with the distributed architecture of the semantic system described by the semantic tile framework. However, the results of the present study also provide evidence of a multimodal hub in ventrolateral ATL, consistent with the hub-and-spoke framework, and evidence that social processing is

subsumed within the semantic system in this hub. These accounts may not be mutually exclusive and the category specialization observed in prior naturalistic work may emerge as a result of the interactions of modality-specialised regions with a deep multimodal hub (Jackson et al., 2021; Rogers & Lambon Ralph, 2022).

We suggest that, during narrative comprehension, the ATL displays differential sensitivity to the type and amount of content being presented, consistent with the hub-and-spoke framework. When the amount of content is high, the ventral ATL region is engaged, when the content is social the dorsolateral and ventrolateral portions are engaged, and when the amount of content is reduced, temporal pole regions are active to facilitate semantic integration with the proceeding narrative context. Taken together, the results call for a revision of the current theories of semantic processing and suggest that, during narrative comprehension, the semantic, semantic control, and social systems are engaged in ways that are not being captured in single word comprehension studies but are nevertheless critical aspects of real-world language processing.

## **Chapter 4**

### **'ALL THE STARS WILL BE WELLS WITH A RUSTY PULLEY': NEURAL PROCESSING OF THE SOCIAL AND PRAGMATIC CONTENT IN A NARRATIVE**

#### **Abstract**

In the real world, language processing is supported by a rich set of verbal and non-verbal contextual constraints. Despite this, the experimental paradigms that predominately informed the current neurobiological model of semantic cognition have tended to present highly decontextualized stimuli. Recent studies using naturalistic stimuli, such as narratives and natural language, report important deviations from this model and suggest that the semantic hub in left anterior temporal lobe (ATL) may display differential sensitivity to the differing demands of narrative comprehension. Specifically, the transmodal hub in ventral ATL may be sensitive to semantic content within the narrative whereas the dorsolateral portion of ATL may primarily respond instead to the quantity of linguistic input. The ventrolateral portion of ATL, centred in the anterior segment of middle temporal gyrus (MTG) and aided by functional connections with the default mode network (DMN), may be additionally engaged by internal processing demands. This may have implications for social processing, which requires access to semantic conceptual knowledge and may drive internal processing during narrative comprehension. How this model of semantic processing extends to more abstract, inferential social processes, such as pragmatic inference, is unclear. The present study examined these issues by quantifying several content types, including semantic, social, and pragmatic content, for each sentence in a complete narrative, *The Little Prince*. In line with the claim that ATL is composed of functional subregions that display differing sensitivity during narrative comprehension, increased activation in ventral ATL was only observed for high semantic (i.e., informative) relative to low semantic sentences. Activation in the dorsolateral and ventrolateral subregions was observed for both high semantic and social conditions relative to the low content sentences, but the ventrolateral ATL effects were more extensive in the social condition. There was high correspondence between the social and pragmatic content results, in particular in the ventrolateral ATL. We argue that social and

pragmatic content drove internal processing that engaged ventrolateral ATL given the pervasive and plot-progressing nature of this content in the narrative. Prior studies using decontextualized stimuli may have missed this functional division within ATL due to minimal internal processing demands. This study provides support for the claim that social processing, including pragmatic inference, engages the semantic system via ventrolateral ATL.

## **Keywords**

*narrative comprehension, naturalistic neuroimaging, social processing, pragmatics, semantic cognition*

## 1 Introduction

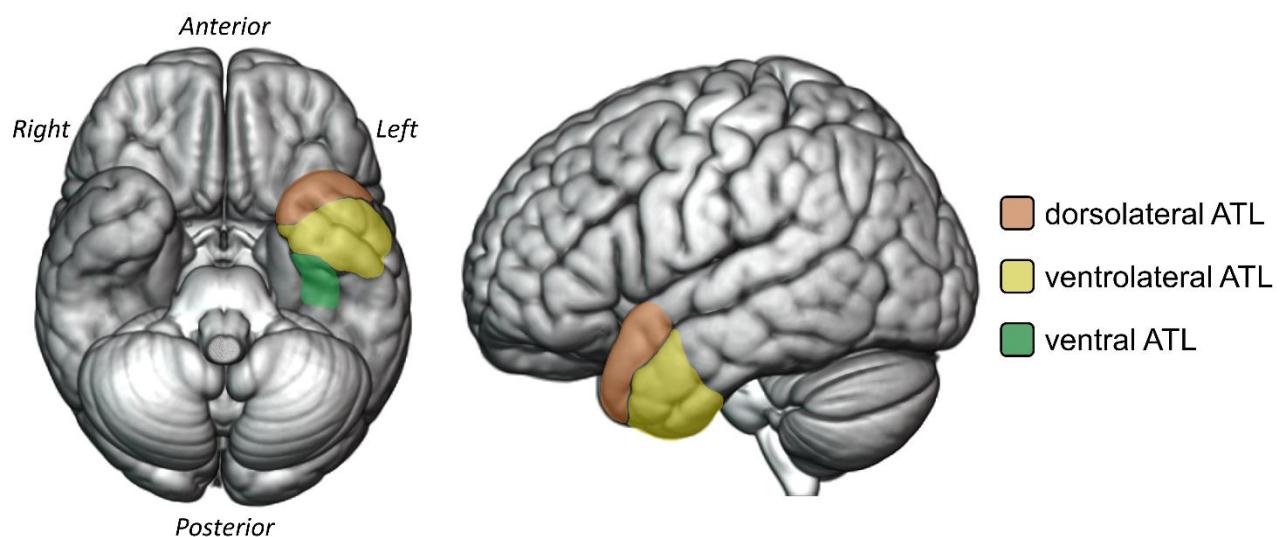
The meaning and impact of natural language and narratives extends beyond the words used to construct the message. Understanding a highly social moment in a narrative, for example, requires integrating the meaning of the words in the current sentence with the prior context and decoding the interpersonal dynamics at play by simulating the mental states of the character(s) (Mar & Oatley, 2008). The context a sentence is embedded within can thus fundamentally change how the meaning is constructed (Deniz et al., 2023; Yee & Thompson-Schill, 2016). When Caesar mutters "*Et tu, Brute?*", the audience understands this to be a highly social and emotional moment, the revelation of betrayal, despite the words in the sentence having minimal emotional valence or arousal. So too does the audience understand that when Marc Antony declares afterwards that Brutus is an honourable man, he means the opposite. Sentences such as these are not rare in narratives or natural language, and, instead, make stories compelling and engaging (Van Duijn et al., 2015).

A key challenge in studying real-world language processing is taking account of how context contributes to the construction of meaning (Xu et al., 2005; Yee & Thompson-Schill, 2016); this is also a core goal of the field of pragmatics (Levinson, 1983). Consider again Marc Antony's declaration about Brutus given above. This moment can only be correctly comprehended if a pragmatic inference is made about how this character feels and what their intentions are in the wake of Brutus' actions. These types of inferences are pervasive in natural language and narratives, and are thought to require mentalizing, and, as a result, engagement of the social cognition system (Levinson, 2006). This is supported by neuropragmatics research (Bambini, 2010; Hagoort & Levinson, 2014) which suggests that pragmatic processing, in particular indirect requests, engage medial prefrontal, bilateral temporoparietal (i.e., TPJ), inferior frontal, posterior cingulate, and precuneus regions (Bašnáková et al., 2014; Licea-Haquet et al., 2021; van Ackeren et al., 2012, 2016). There is, however, variability in the brain areas that support different speech acts. For instance, motor cortex activation is often associated with action-related speech acts due to the fulfilment of the directive whereas more socially complex and indirect speech acts appear to consistently engage the theory of mind network (Tomasello, 2023).

Pragmatic processing is a type of socio-cognitive process that engages the social cognition system, but not all social processing requires inferring communicative intent. Further, the social cognition network includes bilateral temporal poles, bilateral temporoparietal junction (or inferior parietal lobule; IPL), medial prefrontal cortex, anterior cingulate, amygdala, and posterior superior temporal sulcus (Adolphs, 2001, 2009; Frith & Frith, 2007), but the regional response within this network is task-dependent (Breil & Böckler, 2020; Quesque & Rossetti, 2020; Warnell & Redcay, 2019). Meta-analytic evidence shows that even when measuring the same construct, such as mentalizing, presenting the task in a story format and a non-story format elicits different, although partially overlapping, patterns of activation. Distinct subregions within left anterior temporal lobe (ATL) and bilateral TPJ, for instance, are recruited for story and non-story based theory of mind tasks (Mar, 2011). A complicating factor is that social processing includes both conceptual knowledge, which may rely on semantic processing in ATL, and the abstract, inferential applications of that knowledge, which may differentially engage the social, or other cognitive, systems.

A recent theoretical account argues that social knowledge is housed within the semantic system, leveraging the neural architecture of the semantic and semantic control systems (Binney & Ramsey, 2020; Diveica et al., 2021). Critically, there is strong evidence that social concepts engage the ATL, in line with the role of this region as a hub for semantic representation (Binney et al., 2016; Rice et al., 2018; Zahn et al., 2007). The ATL is large, however, and displays graded functioning driven by variations in connectivity with distal modality-specific spoke regions (Binney et al., 2012; Rice et al., 2015). The ventral portion of ATL, centred in left anterior fusiform gyrus, is most consistently implicated as the transmodal hub that receives equal inputs from the surrounding sensorimotor spokes (Lambon Ralph et al., 2017). ATL regions proximal to this hub appear to display varied semantic specialization, although their anatomical definitions can vary across studies. The anatomical definitions of three key ATL subregions are provided in **Figure 1** and can be summarized as follows: the *dorsolateral* portion contains the anterior segment of superior temporal gyrus (STG), the *ventrolateral* (or inferolateral) portion contains the anterior segments of middle and inferior temporal gyri (MTG, ITG), and the *ventral* portion contains the anterior segment of fusiform gyrus. Social knowledge, along with

many other types of concept, appears to engage the ventrolateral portion of ATL and there is some evidence for specialization for social knowledge in the dorsolateral ATL (Binney et al., 2010; Olson et al., 2013; Zahn et al., 2007). A cross-task investigation of abstract social processing (i.e., theory of mind reasoning), for instance, found overlap in the ventrolateral portion of ATL (Balgova et al., 2022). This same region, alongside the dorsolateral ATL region, shows increased activation in response to social and social-emotional sentences (Mellein et al., 2016).



**Figure 1. Anatomical definitions of ATL functional subregions.**

A slightly different pattern is observed in naturalistic contexts, however. The dorsolateral ATL appears to be more robustly engaged than other subregions within ATL during natural language or narrative comprehension, and ventral ATL seems particularly sensitive to semantic input (Malik-Moraleda et al., 2022; Wu et al., 2022). Conversely, the ventrolateral ATL is engaged by social language in narrative and movie contexts after controlling for the quantity of words (Thye et al., 2023)([Chapter 5](#)). These results suggest a functional distinction in which the dorsolateral and ventral ATL are particularly sensitive to external linguistic processing, driven by the quantity and informativeness of input stimuli, respectively, whereas the ventrolateral ATL, through functional connections with the default mode network (DMN) (Lee et al., 2020; Raichle, 2015), is sensitive to internally-driven semantic processing,

requiring the accumulation and integration of conceptual knowledge about the narrative. We refer to this internally-driven processing hereafter as *endogenous semantic processing*. Naturalistic studies of social processing rarely control for externally driven semantic demands, which makes it difficult to determine why ventrolateral ATL responds preferentially to social content (relative to non-social content) but also to non-social semantic content (relative to non-semantic content). When external semantic input is controlled, we might then still expect engagement of ventrolateral ATL in conditions that require introspection or reflection on the narrative events and incorporation of new information into the ongoing situation model, which social content might elicit.

These claims are about the literal content of narratives and do not account for or make any predictions about pragmatic processing, which requires inferences beyond the literal content. That is, sentences where representation of the concepts in the sentence – which models of semantic cognition are concerned with – is not sufficient for comprehension. Instead, the lexical-semantic knowledge must be integrated with a situation model of the overarching context or narrative (Yarkoni et al., 2008; Zwaan & Radvansky, 1998), and an inference must be made that runs counter to the conceptual representation. It may be that the semantic system in ATL is for processing literal content and pragmatic processing relies on other brain regions. Alternatively, social processing and pragmatic inference may both engage ventrolateral ATL because both require reflecting on and integrating the local information with the global context. This claim builds on prior work arguing that social processing is, at least partially, subsumed within the semantic system, but there have been limited tests of this specific claim using protracted narrative stimuli and no investigations of whether this extends to pragmatic processing.

Narratives provide an ideal avenue to explore this account. First, they more closely approximate everyday language comprehension (Sonkusare et al., 2019). Studies using naturalistic stimuli such as narratives suggest that current neurobiological models of semantic and, more broadly, language processing are impoverished estimates of how these systems are engaged in real-world contexts (Deniz et al., 2019; Huth et al., 2012, 2016; Ross et al., 2022). Despite this, studies of social cognition have predominately used non-naturalistic stimuli that minimally incorporate context to capture social or pragmatic processing (Redcay &

Moraczewski, 2019). There is a need to use more ecologically valid stimuli to better inform current models of human cognition. Second, narratives have nested, contextualized feature layers that facilitate sampling at different levels of meaning (Willems et al., 2020). For instance, comprehension can be measured from the word and sentence level up to the level of character actions and narrative events. Each feature layer incorporates more context, allowing for an empirical test of social and pragmatic content. Studies explicitly manipulating context by presenting scrambled words, sentences, or paragraphs extracted from a narrative suggest that sentence-level processing, and possibly social processing in particular (Zhang et al., 2021), engages bilateral ATL and left IPL whereas narrative processing engages a similar, but more broad network including medial prefrontal regions, right IPL and precuneus (Hasson et al., 2008; Lerner et al., 2011; Xu et al., 2005). It is unclear to what extent these regions are differentially engaged in response to the social content within the narrative and whether context manipulations invariably impact how narrative content is processed.

Despite the critical role of context in pragmatic processing, few, if any, studies have investigated pragmatic processing during narrative comprehension. This is likely due to the fact that unlike socialness and the other content types investigated here, pragmatic content cannot be quantified at the lexical-level because the required inference occurs at higher feature layers in the narrative which incorporate context (Bambini, 2010; Hagoort & Levinson, 2014). Further, studies have tended to use an active task (e.g., classification or recognition judgment) or a baseline condition that does not isolate the effect of interest (e.g., manipulation of ambiguity in prosodic expressions) (Hellbernd & Sammler, 2018) to study pragmatic processing. It has been suggested that a passive task, which narrative comprehension provides, may reduce conflation with other higher order cognitive functions involved in completing the task (Tomasello, 2023).

A natural extension of the prior work on social and pragmatic processing is to select a feature layer that accommodates some context: sentences. Sampling content at the sentence-level is advantageous because sentences are nested within the middle of the narrative hierarchy, so the local context is incorporated while providing some level of constraint (Willems et al., 2020). There are several approaches to representing sentence-level content. Perhaps the most common are

through the application of large language model (LLM) embedding models or by aggregating features of the words used in the sentence (Anderson et al., 2017). These approaches do not take narrative context into account, thus failing to capitalize on the full context afforded by measuring sentence-level content embedded in a narrative. An alternative approach is to obtain subjective sentence ratings on a continuous basis from novice or trained raters. A key benefit of this approach is that sentences are not treated as independently sampled from the narrative. This allows for preceding context to impact the rating, an important step toward capturing narrative comprehension as it actually happened. Further, as experts in natural language comprehension, human raters are well-suited to making these types of judgments.

Prior studies using subjective sentence or passage-level ratings have focused on either emotional or social content in isolation (Bestgen, 1992; Hsu et al., 2015; Zhang et al., 2021). This approach has several limitations. The first is that it is agnostic to the relationship between social or emotional content, which are likely to be correlated in narratives. Distinguishing – or quantifying the relationships – between these and other content types is critical for making strong inferences about social or emotional processing, respectively. The second limitation of the approach taken in prior studies is that the ratings were made using excerpts or shorter passages, which reduces the influence of context on the subjective assessments. Using a complete, protracted narrative with sentences rated consecutively (as opposed to in a random order) better captures the type and extent of content present across the narrative. This is particularly relevant for quantifying social and pragmatic content, which are strongly influenced by both the local and global context of the narrative: relationships between characters and the reader's understanding of their motives and intentions evolve over the course of the narrative. This information is difficult (perhaps impossible) to capture when sentence-level content is quantified outside of its full narrative context.

In the present study, content ratings were obtained for each sentence in a complete narrative, *The Little Prince*. We previously analysed this same narrative using the *Le Petit Prince* publicly available dataset (Li et al., 2022), focusing on the neural processing of the lexical-semantic properties of the words that comprise the narrative (Thye et al., 2023). We found support for the claim that social language

engages the semantic system in ATL – activation in both the dorsolateral and ventrolateral portions positively covaried with social content. The ventral ATL hub was engaged when semantic content (i.e., number of content words) increased, but the rest of the ATL was engaged during narrative moments when fewer content words were present. We suggested that these moments provided listeners a chance to “catch-up” or integrate the narrative information into their ongoing situation model – in other words, to engage in endogenous semantic processing. The present study extends this work by examining representation of the narrative in a broader sense, moving from word-level representation to sentences, which allow for context to influence meaning.

The primary aims of the present study were (1) to evaluate the hypothesis that social processing during narrative comprehension is supported by the semantic system and, if it is, clarify which subregion(s) of ATL are engaged by social content, and (2) to examine semantic and social network engagement for pragmatic processing, a socio-cognitive process that does not rely on explicit access to conceptual knowledge. The social and pragmatic content of sentences were thus coded separately to make it possible to separate and compare them.

Subjective sentence content ratings provide moment-by-moment approximations of social and pragmatic processing during narrative comprehension. Using these ratings, we are able to test competing accounts. The first account, the *graded hub hypothesis*, suggests that social information, like other types of semantic information, is processed within a domain-general ATL hub (Balgova et al., 2022; Lambon Ralph et al., 2017). This account would predict that, when the amount of semantic input is matched, there should be approximately equal activation in high and low social conditions. As a result, we would expect minimal effect on ventral ATL activation, because the semantic content is balanced across conditions so transmodal hub activation should be the same, and instead, anticipate activation in dorsolateral ATL given prior research showing sensitivity to socialness in this region in response to non-naturalistic stimuli (Olson et al., 2013; Zahn et al., 2007). The alternative, *endogenous semantic processing* extension of the graded hub hypothesis discussed above, would instead predict that ventrolateral ATL should respond particularly strongly to sentences with highly social content on the presumption that social content is salient to the narrative and requires endogenous processing. In contrast, if

dorsolateral ATL is primarily sensitive to quantity of semantic input, when the amount of external semantic input is matched, engagement of dorsolateral ATL should be balanced across conditions and subtracted out. Listening to sentences with highly pragmatic content was also expected to engage the social cognition network brain regions in right supramarginal and angular gyri (i.e., TPJ), given the role mentalizing plays in making pragmatic inferences. A final, exploratory aim of the study was to examine the extent to which social and pragmatic content displayed shared engagement of the semantic cognition system in left ATL.

### 1.1 *Related content types*

To address the limitations of prior work and comprehensively characterize sentence-level content, several related content types were rated alongside social and pragmatic content.

**Semantic.** Sentence-level semantic content was coded as a baseline measure of general narrative comprehension. The definition used in the current study was designed to capture engagement of the semantic system in response to highly informative sentences. Recent studies of narrative or natural language comprehension have called into question the neural basis of semantic cognition. In contrast to the hub-and-spoke framework in which information from sensorimotor spokes is integrated in a transmodal hub within ATL (Lambon Ralph et al., 2010, 2017), the semantic tile framework, motivated by naturalistic investigations of the semantic system, argues that semantic specialization is tiled throughout the cortex and does not display a hub architecture (Huth et al., 2012, 2016). Although these accounts may not be mutually exclusive (Rogers & Lambon Ralph, 2022), there is a need to investigate how semantic processing occurs in real-world contexts, such as narratives. In addition to reconciling these ostensibly opposing neurobiological models of semantic cognition, coding both semantic and social sentence-level content allows for an empirical test of whether they engage the same transmodal hub in ventral ATL.

Listening to sentences with high semantic content was expected to engage a broad language network, consistent with prior studies of narrative comprehension (Malik-Moraleda et al., 2022; Thye et al., 2023; Zhang et al., 2020). Engagement of

ventral ATL in response to highly semantic content would provide support for the graded hub hypothesis, suggesting this region serves as a cross-model hub for semantic processing (Balgova et al., 2022; Lambon Ralph et al., 2017). Alternatively, because informativeness ratings closely approximate the external semantic input and minimally capture endogenous processing demands, engagement of dorsolateral ATL (and not ventrolateral ATL) would provide support for an anatomical distinction between processing semantic input (dorsolateral ATL) and engagement for both semantic input and endogenous semantic processing (ventrolateral ATL).

**Ambiguous.** Sentences can be ambiguous when they have multiple or unclear meanings, or complex syntax that is difficult to parse. Resolving sentence-level ambiguity requires the semantic control system to facilitate selection of the appropriate meaning from multiple possible targets (Rodd et al., 2012; Vitello & Rodd, 2015). Semantic control is the ability to select appropriate, task-relevant conceptual information, inhibit or filter out unrelated or extraneous information, and resolve ambiguities in language (Jackson, 2021). In the present study, ambiguity was defined as having multiple interpretations, including syntactic and semantic ambiguity, which are common manipulations of sentence-level ambiguity that engage left IFG (Rodd et al., 2010). The definition also included the use of non-literal, or figurative, language which, in addition to having multiple possible interpretations, engages the semantic control network in left IFG (Hauptman et al., 2023; Nagels et al., 2013). Importantly, this definition did not include the use of irony or sarcasm, which has been shown to require socio-cognitive processing and pragmatic inference and recruit regions within the social cognition network (Bohrn et al., 2012; Spotorno et al., 2012). Given this, irony and sarcasm were instead coded as pragmatic content in the present study.

Meta-analytic evidence suggests that distinct domains of socio-cognitive processing (e.g., empathy, theory of mind) require the semantic control system, in particular the anterior inferior frontal gyrus (IFG) (Diveica et al., 2021). This may indicate that social processing places increased demands on the semantic control system, an inference supported by greater activation within this network in response to social relative to matched, non-social concepts (Binney et al., 2016). Alternatively, prior studies examining social processing (with verbal or non-verbal stimuli) may not have appropriately matched the conditions on semantic control demands, limiting the

conclusions that can be made about semantic control system involvement in socio-cognitive processing. Further, the engagement of the semantic control network has been minimally investigated in response to naturalistic social processing. To address this limitation, sentence-level ambiguity was coded to allow sentences with high versus low social and pragmatic (or other) content to be matched on general semantic control demands.

Highly ambiguous sentences were expected to engage left IFG and posterior middle temporal gyrus (MTG), given the role of these regions in resolving sentence-level ambiguity (Vitello & Rodd, 2015). For high versus low social content sentences, matched on ambiguity, any observed inferior frontal activation would indicate that socio-cognitive processing places increased demands on the semantic control system.

**Emotional.** Social and emotional sentence-level content were coded independently given the anticipated coupling of these content types in narratives. Emotional content is conceptually separate from social content, processed within a distinct brain network (Kotz & Paulmann, 2011), and can be elicited by social or non-social information. However, narratives tend to over-sample emotionally salient social information which can make differentiating the content types at the sentence level challenging. Capturing sentence-level emotional content has the additional advantages of allowing higher level features, such as prosody, to influence content ratings and being comparable to prior research that made use of subjective sentence and passage-level emotion ratings (Bestgen, 1992; Hsu et al., 2015).

Highly emotional sentences were expected to engage amygdala, insula, cingulate cortex, and prefrontal regions based on prior research (Citron, 2012; Cunningham et al., 2004; Vigliocco et al., 2014).

## 2 Methods

### 2.1 Dataset

The present study used the publicly available *Le Petit Prince* dataset (<https://openneuro.org/datasets/ds003643/versions/1.0.4>) (Li et al., 2022). This dataset is ideally suited for testing hypotheses related to semantic processing given the use of a multi-echo functional sequence that enhances signal in ventral aspects

of ATL, the core semantic hub region. The pre-processed data were selected for the English-speaking participants who listened to *The Little Prince* audiobook during MRI scanning ( $n=48$ ; 29 female;  $M_{age}=21.33$ ). The audiobook duration was 94 minutes, and the book was presented in nine approximately 10-minute functional runs (range: 8:42 – 12:07 minutes), interspersed with comprehension questions about the preceding excerpt. Participants gave written informed consent prior to participation and were paid, in accordance with the IRB guidelines of Cornell University.

## 2.2 *Narrative segmentation*

The first author segmented the narrative into sentences using the audio files provided with the dataset. This was done using version 3.0.2 of Audacity© (Audacity Team, 2021). Where ambiguous, sentence boundaries were confirmed via visual inspection of the waveform. Each sentence was saved as a separate audio file to ensure that ratings were given in response to the same content, as opposed to having raters pause the narrative after each sentence. None of the superfluous audio was removed. Where neutral pauses between sentences occurred, the inter-sentence interval was divided roughly evenly between the prior and subsequent sentence. Where pauses for reflection or emphasis occurred (based on the judgment of the listener), the pause was preserved in the affected, usually preceding, sentence.

Event segmentation was done jointly with sentence segmentation following the principles outlined in prior research (Radvansky & Zacks, 2017; Shin & DuBrow, 2021). These principles suggest that information within an event is more predictable than information between events – any sudden or unexpected shift that made the narrative seem discontinuous was an indicator that a new event has begun. This shift could be in setting, emotional tone, character involvement, or action sequence, but, regardless of the source, the shift was used to define discrete boundaries around the meaningful events in the continuous narrative. The segmented narrative was comprised of 1,230 sentences and 40 events; each event contained between 8 and 80 sentences. The same event and sentence segmentation procedure was applied, where needed, to three practice narratives: a story from the NyU-BU Contextually Controlled Stories Corpus (Lewis et al., 2020) (133 sentences, 20 events), *The Steadfast Tin Soldier* (110 sentences, 8 events), and *The Town*

*Musicians of Bremen* (74 sentences, 6 events). The latter two practice narratives were chosen as close approximations of *The Little Prince* in reading level, genre, and narrator (both female).

## 2.3 Content types

Sentences were coded on five content types: semantic, social, pragmatic, ambiguous, and emotional. A detailed protocol with descriptions of the content types with example low, moderate, and high sentences and instructions on how to rate the sentences and describe events is shared on the project OSF page ([https://osf.io/8c6nf/?view\\_only=b1471ce0572a4c098878bf82202b7b6a](https://osf.io/8c6nf/?view_only=b1471ce0572a4c098878bf82202b7b6a)). The initial version of the protocol was drafted by the first author and refined with the input of last author and 4 volunteer raters while coding the three practice narratives. The protocol was finalized prior to coding *The Little Prince*.

For the present analysis, the content coding was done using a categorical scale in which sentences were placed into low, moderate, or high categories for each content type. The sentence coding was done by the first author who developed the protocol and coded the practice narratives. To validate the coding approach, approximately 5% of the sentences (n=70) were semi-randomly selected, oversampling high content ratings, for review by the last author. To validate the assignment of sentences to categories, the 4 volunteer raters, trained using the protocol and the practice narratives, provided numeric ratings for all narrative sentences. The correspondence between the numeric and categorical coding approaches was high: there was a significant categorical condition difference (i.e., high vs low) in the numeric ratings across all content types. The details of this validation analysis using numeric ratings is provided on OSF and as supplementary information ([Appendix C: Supplemental Figure 1](#)).

**Semantic Content.** To differentiate sentences with relatively high vs low semantic content, we defined semantic content based on how informative the sentence was. The amount or importance of the information conveyed was used to distinguish sentences. A high semantic sentence would move the story forward in a significant way, bring together plot points, or give the reader more information about the characters or event. The protocol explicitly stated that longer sentences should

not be given higher scores just because they are longer; although these sentences, due to their length, might contain more information on average. Definitions, or explanations of the meaning of a word or event, were always coded as at least moderately semantic, even if the definition was already known. The familiarity of a setting or situation might decrease the score, however. A familiar scene (e.g., description of a desert) might receive a lower semantic score than a highly unfamiliar scene in which the information cannot be anticipated or understood without explanation (e.g., description of the prince's planet). This is because no familiar image or understanding of the context can be relied upon, so the information must be processed more deeply.

Sentences in which new information is presented were coded as more semantic than sentences with information that is already known to the reader. This was done because the reader is updating their understanding of the events within the narrative as the narrative unfolds, so newly presented semantic content is more impactful or significant when first introduced. This information is considered "new" only if it is being presented to the reader for the first time. Sentences in which a character learns information the reader already knows were not rated as highly semantic. Sometimes these sentences are used to increase the drama, emotion, or social significance of the event. In cases when re-presented information is used in this way, the semantic score may be low to moderate, but the social, emotional, or pragmatic score may be moderate to high.

**Social Content.** Sentences were considered social if they involved or related to the characters in the narrative. In particular, socialness was defined as the way the characters interact together, how they understand the thoughts, beliefs, and motives of the other characters in their environment, and how the characters themselves behave in relation to the others in the environment. This included interactions between the reader and the narrator if, for instance, the narrator addresses the reader directly. The relative degree of social content depended on the type, duration, and significance of the interaction. Deeper interpersonal interactions or interactions that were significant because of the specific characters in the sentence were considered highly social. Social content was considered independently from emotional content, although a sentence may be both highly social and emotional.

We anticipated that capturing social content at the sentence-level may be potentially stymied by the presentation of social interactions in an audiobook in which one character speaks at a time. As a result, isolated sentences rarely contain character interactions. The interaction instead occurs over the course of several sentences, possibly capturing a dialogue between characters. Further, when an interaction is described by a narrator, social moments may feel impersonal or detached. To avoid underestimating social content, sentences in which a character is talking to or replying to another character or in which the narrator is describing a social interaction were considered at least moderately social. In addition, the preceding context was considered in rating all content types, but these properties of social interactions in audiobooks was further emphasized in the protocol.

**Pragmatic Content.** Pragmatic content was defined as requiring reasoning or extrapolation beyond the literal meaning of the words in the sentence. Highly pragmatic sentences require an inference based on an understanding of the communicative intent of the character, narrator, or author and are context dependent; the words of the sentence imply one meaning, but understanding the character's beliefs or attitudes changes the interpretation. As such, highly pragmatic sentences are those that would be incorrectly understood if extracted from the narrative and presented in isolation.

To aid in differentiating ambiguous and pragmatic content, we noted that highly ambiguous sentences can have multiple possible interpretations, but highly pragmatic sentences have one correct interpretation that requires an inference to be made. Further, despite requiring a non-literal interpretation of the language used, sentences with figurative language were not considered pragmatic unless understanding the meaning required additional context about the prior events or characters. Given the ubiquity of pragmatic inference in everyday conversation and story-telling, it did not matter how easy or automatic the pragmatic inference was. Whether a sentence received a moderate or high pragmatic rating depended instead on the necessity of the inference to correctly understand the meaning of the sentence.

**Ambiguous Content.** Sentences were considered ambiguous if they were confusing or vague. This definition was further divided into three types of ambiguity. The first was whether the sentence had multiple possible interpretations, such as

figurative language, in which there is not one correct interpretation. Readers may interpret these types of sentences slightly differently, so it is not straightforwardly clear what the character, narrator, or author is saying without thinking through the possible interpretations. The second type, syntactic ambiguity, was how difficult or effortful the meaning of sentence was to work out. These types of sentences may have an unusual syntactic construction, possibly with embedded clauses, that make it challenging to immediately understand. This ambiguity might be resolvable by re-listening to the sentence, and the meaning of the sentence may not be ambiguous (i.e., what is described is exactly what happened), but the structure of the sentence resulted in initial confusion or required effort to comprehend. The third type, narrative ambiguity, occurs when it is not clear to the reader what is happening. For instance, the sentence may suggest that something unexpected happened (e.g., a loud noise), but there is not enough information to work out the details of what occurred. Re-listening to the sentence would not resolve this type of ambiguity and would instead require additional information from subsequent sentences. A sentence containing any of these types of ambiguity was rated as moderately to highly ambiguous.

**Emotional Content.** Emotional content was defined as how poignant a sentence is or the extent to which it relates to or evokes intense feelings. These strong feelings could be positive (e.g., joy, affection, excitement) or negative (e.g., heartbreak, regret, longing) and be experienced by a character, the narrator, or the reader. The relative intensity of the emotion described or felt determined whether the sentence was rated as highly emotional. Simple, less poignant sentences that state emotion explicitly (e.g., ‘I was mad’) were not given higher emotional content scores just because an emotion is named. Conversely, an emotion did not have to be explicitly named in the sentence for a sentence to be considered highly emotional. Some inference may be required to understand that a character is experiencing an emotion. This type of sentence may be considered both moderately pragmatic and emotional.

## 2.4 Content coding

Sentence content ratings were made using a survey generated in Qualtrics. For each sentence, the audio file was presented at the top of the page, and a matrix table with rows corresponding to each content type and columns corresponding to

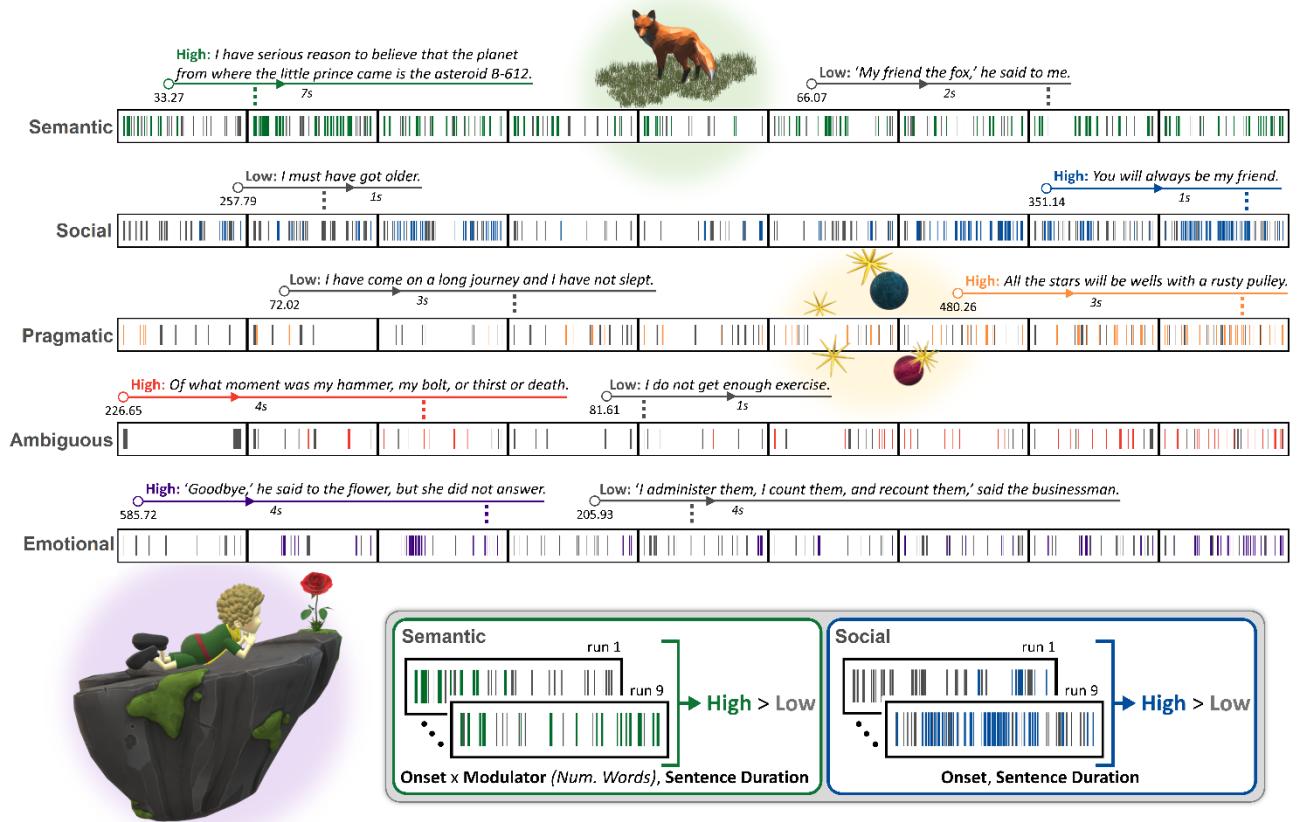
the rating was presented below the audio file. Raters were able to listen to the sentence multiple times, if desired. This was done to facilitate independent reflections of each content type. In other words, the rater could listen to the sentence five times, thinking about a different content type after each listen. Limiting the raters to only 1 playback would have prioritized the first content type rated. Each sentence was presented on a separate page of the survey. Raters could navigate to prior sentences but were instructed to not revise ratings based on subsequent sentences. The content coding was done for all of the sentences within an event in one sitting without breaks to preserve the context as much as possible. After each event, raters were prompted to ‘Describe what happened during the event, including things that happened that were not explicitly described’. This allowed for a comprehension check and a comparison of the salient features of the event, including any pragmatic inferences made, across raters.

## *2.5 Sentence matching*

After the content coding was complete, the high content sentences for each content type were selected for analysis. Potential matched low content candidate sentences were identified using number of words and sentence duration, calculated from the onset of the first word to the offset of the last word in the sentence. A 1:1 matching approach was then implemented: for each high content sentence, an approximately-matched low content sentence was selected from the list of candidates. In addition to number of words and duration, the sentences were matched, where possible, on the other content types to reduce confounding effects (e.g., high and low semantic content sentences were matched on social, pragmatic, ambiguous, and emotional content).

## *2.6 Neuroimaging analysis*

See **Figure 2** for the distribution of matched sentences within the narrative, example High and Low sentences for each content type, and an overview of the analysis.



**Figure 2. Distribution of sentences in narrative.** The elongated horizontal bars show the full narrative divided into the nine approximately 10-minute long runs. Within each horizontal bar, the darkly coloured vertical lines (green for semantic, blue for social, orange for pragmatic, red for ambiguous, purple for emotional) correspond to the High content sentences, and the dark grey vertical lines correspond to the Low content sentences. The width of the lines is determined by sentence duration. Example High and Low content sentences are highlighted for each content type with a dotted line indicating their temporal position in the narrative. The number underneath the open circle indicates the onset time of the first word in the sentence relative to the beginning of the functional run. Sentence duration is indicated in italics underneath each highlighted sentence. A schematic of the analysis pipeline is provided at the bottom of the figure to illustrate the differences between the Semantic content (which included a modulator for number of words) and the rest of the content types (Social is shown as an example).

The pre-processed data were used for analysis, and the MRI acquisition parameters and pre-processing pipeline are outlined in the paper describing the dataset (Li et al., 2022). Briefly, anatomical data were skull-stripped and spatially normalized to the same stereotaxic space (MNI). Functional images were processed through a standard pre-processing pipeline which included slice-time correction, despiking, co-registration to the anatomical image, and normalization to MNI space. Functional images were acquired using a multi-echo EPI sequence and multi-echo independent component analysis was used to remove noise and motion artefacts.

To examine neural processing across content type, duration modulated event related analyses were run in AFNI (Cox, 1996). The 9 functional runs were first scaled such that each voxel had a mean of 100 and then concatenated to generate a single time course for each participant. For each content type, the onset of the high or low sentences with respect to the start of the run and the sentence duration were modelled. For the semantic content analysis, the number of words was included as a modulating variable to regress out any differences due to sentence length.

A linear mixed effects model with a fixed effect of content type and random effect of subject was run with the subject level activation maps from each content type condition as inputs using 3dLMEr (Chen et al., 2013). The simple effects of High > Low content was extracted from the model estimates for each content type. Permutation based cluster correction was implemented using 3dClustSim (Cox et al., 2017) based on the spatial smoothness of the residuals file. This yielded a cluster size of 168 based on bisided first-nearest neighbour clustering (NN1) and an uncorrected voxelwise threshold of  $p < .05$  and a cluster forming threshold of  $p < .01^1$ . The resulting cluster size threshold was applied to the group level activation maps for each High > Low content contrast. Results figures were generated using MRIcroGL (Rorden & Brett, 2000). All analysis code, study materials, and supplementary information are available on Open Science Framework: [https://osf.io/8c6nf/?view\\_only=b1471ce0572a4c098878bf82202b7b6a](https://osf.io/8c6nf/?view_only=b1471ce0572a4c098878bf82202b7b6a).

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<sup>1</sup> Given that the resulting networks were relatively extensive, we also applied a more conservative threshold derived from an uncorrected voxelwise threshold of  $p < .01$ . These results are highly consistent with those reported in the results sections and are shared on OSF and as supplementary information ([Appendix C: Supplemental Figure 2](#)).

### 3 Results

#### 3.1 Sentence matching

The categorical coding approach identified 120 semantic, 212 social, 77 pragmatic, 46 ambiguous, and 99 emotional sentences with high content ratings. Well-matched low content sentences were not available for 19 of the high social and 5 of the high semantic content sentences, so these were removed from analysis. The final analysis consisted of 230 semantic (115 high; 115 low), 386 social (193 high; 193 low), 154 pragmatic (77 high, 77 low), 92 ambiguous (46 high, 46 low) and 198 emotional (99 high, 99 low) stimuli. Some sentences were used to capture more than one (high or low) content type.

Sentence matching was checked using two sample *t*-tests to compare the continuous variables (number of words and sentence duration) and Fisher's Exact Test to compare the categorical variables (other content type ratings) in the High versus Low conditions. With the exception of semantic sentences, the within content type high and low sentences were matched on number of words and sentence duration. Unsurprisingly, it was not possible to match high and low semantic sentences on these variables: the high semantic sentences, on average, had more words and were longer in duration than the low semantic sentences. In matching across the other content types, social and emotional ratings were highly correlated and could not be manipulated independently. In other words, highly social sentences were also frequently moderately to highly emotional, and there were relatively few low social sentences that were also moderately to highly emotional for matching. The analogous was true for emotional content: there were fewer high social, low emotion sentences than there were high social, high emotion sentences. Apart from this, the high and low sentences were well-matched across all content types ( $p > .05$ ). See **Table 1** for the detailed condition matching information.

**Table 1***High and low content sentence matching*

	Num. words	Duration	Semantic			Social			Pragmatic			Ambiguous			Emotional		
			L	M	H	L	M	H	L	M	H	L	M	H	L	M	H
<b>Semantic</b>																	
High	24.61	7.93	-	-	<b>115</b>	49	49	17	100	9	6	93	17	5	84	23	8
Low	12.09	3.94	<b>115</b>	-	-	49	49	17	100	9	6	93	17	5	86	23	6
p	<.001	<.001				1			1			1					0.92
<b>Social</b>																	
High	13.65	3.99	67	108	18	-	-	<b>193</b>	163	18	12	165	24	4	32	111	50
Low	13.41	4.06	62	105	26	<b>193</b>	-	-	164	22	7	164	22	7	135	42	16
p	0.75	0.81			0.44				0.43			0.70					<.001
<b>Pragmatic</b>																	
High	12.62	3.90	41	30	6	7	42	28	-	-	<b>77</b>	75	2	0	45	22	10
Low	12.84	3.88	38	34	5	7	43	27	<b>77</b>	-	-	73	3	1	45	22	10
p	0.85	0.95			0.82			1				0.68					1
<b>Ambiguous</b>																	
High	15.00	4.74	12	29	5	18	24	4	44	2	0	-	-	<b>46</b>	30	15	1
Low	15.39	4.64	12	29	5	17	25	4	41	4	1	<b>46</b>	-	-	35	10	1
p	0.83	0.86			1			1		0.43			-			0.67	
<b>Emotional</b>																	
High	11.80	3.55	43	48	8	<b>17</b>	26	56	79	10	10	91	7	1	-	-	<b>99</b>
Low	11.88	3.61	45	46	8	18	64	17	81	9	9	93	5	1	<b>99</b>	-	-
p	0.94	0.86			1			<.001		0.93		0.88					-

Note. Num., Number. L, Low. M, Moderate. H, High. Within condition high and low sentence values are bolded. Red shading indicates a lack of matching between the low and high sentences for a given content type.

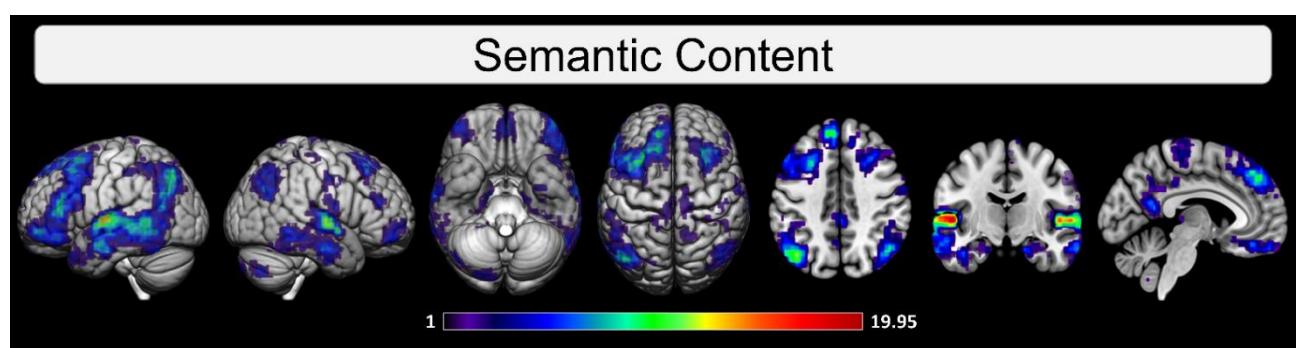
### 3.2 Neuroimaging analysis

The coordinate information for all results is provided in **Table 2**.

#### 3.2.1 Semantic content

Listening to sentences with high compared to low semantic content was associated with activation in a large, bilateral network (**Figure 3**). This network appeared to overlap considerably with, although was more extensive and bilateral than, the ‘universal’ language network identified using localizers across a diverse set of languages (Malik-Moraleda et al., 2022).

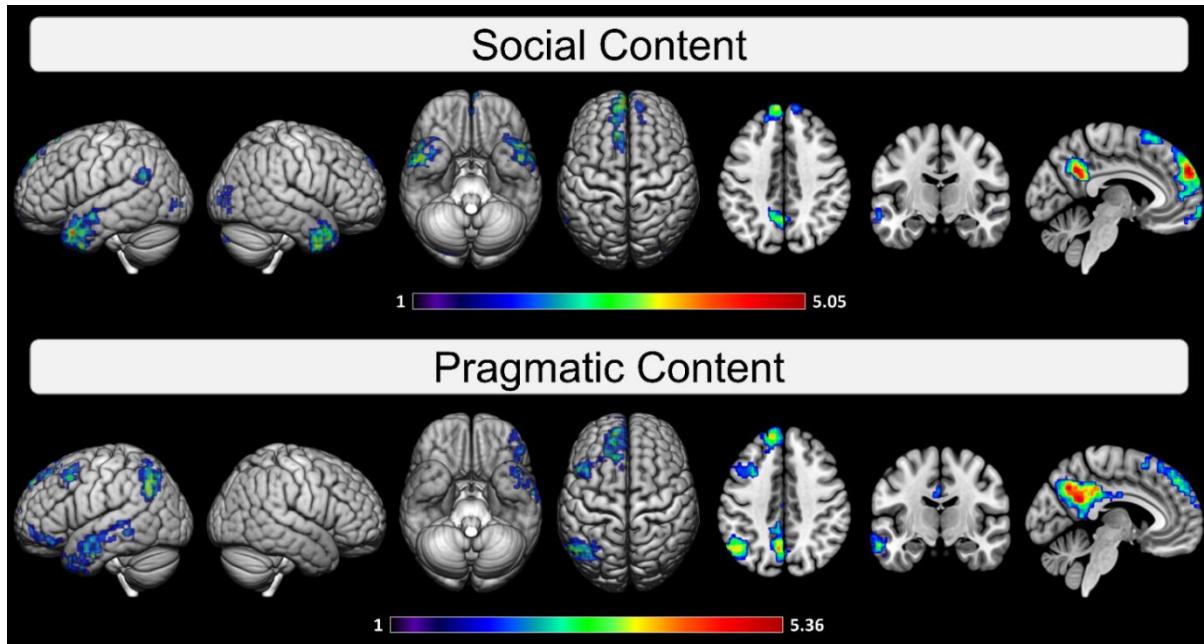
Specifically, high semantic content was associated with left ventral ATL (fusiform gyrus) and lateral temporal and parietal activation extending from a superior portion of ATL posteriorly into superior, middle, and posterior inferior temporal gyri, inferior parietal lobule and postcentral gyrus. There were comparatively smaller right hemisphere clusters of activation in inferior, middle, and superior temporal gyri and fusiform and in right inferior parietal lobule and portions of postcentral gyrus. There was frontal activation in left inferior, middle, and superior frontal gyri, and smaller clusters in analogous right hemisphere frontal regions. Activation in hippocampus, middle cingulate cortex, precuneus, and both cerebellar hemispheres was additionally observed for high versus low semantic content sentences.



**Figure 3. High > Low semantic content results.** Thresholded Z-score statistical map showing lower (purple) to higher (red) values.

### 3.2.2 Social content

Listening to sentences with high compared to low social content was associated with activation in left superior (i.e., dorsolateral) ATL and bilateral ventrolateral ATL as well as left angular gyrus, superior medial gyrus, precuneus, inferior occipital gyrus, and the right posterior lobe of the cerebellum (**Figure 4**).



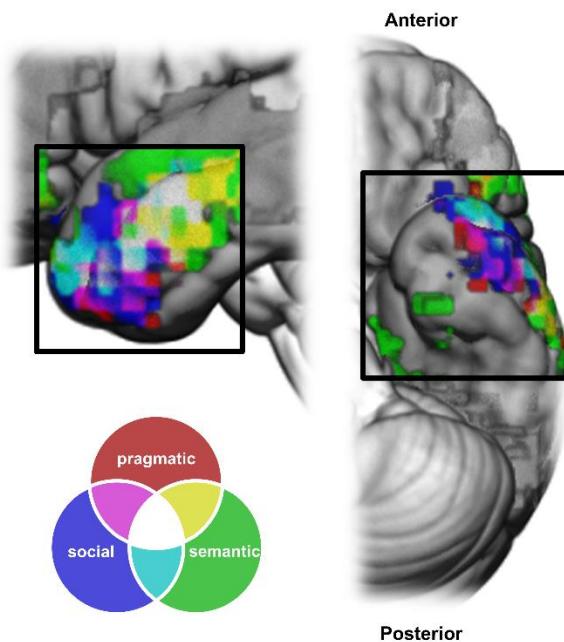
**Figure 4. High > Low social and pragmatic content results.** Thresholded Z-score statistical map showing lower (purple) to higher (red) values.

### 3.2.3 Pragmatic content

There was high correspondence between the social content and pragmatic content results. Listening to sentences with high compared to low pragmatic content was similarly associated with activation in left ventrolateral ATL, a small portion of dorsolateral ATL, left angular gyrus, precuneus, and left superior medial gyrus (**Figure 4**). The results were left lateralized, however, with no associated right ATL activation. In addition, high versus low pragmatic content was associated with activation in left middle frontal gyrus and the orbitalis portion of left inferior frontal gyrus. Importantly, the similarity between the left hemisphere regions engaged by social and pragmatic content was observed despite the fact that the content types were orthogonally manipulated. Social content was matched between the high and

low pragmatic sentences, and, inversely, pragmatic content was matched between the high and low social sentences.

There was overlapping and differential engagement of the ATL subregions for semantic, social, and pragmatic content (**Figure 5**). Only semantic content engaged ventral ATL, whereas both semantic and social content engaged dorsolateral ATL. Only pragmatic and social content engaged the same anterior portion of ventrolateral ATL, centred on anterior MTG. A slightly posterior portion of anterior MTG (ventrolateral ATL) showed overlapping sensitivity for all three content types: general semantic, social, and pragmatic inference.

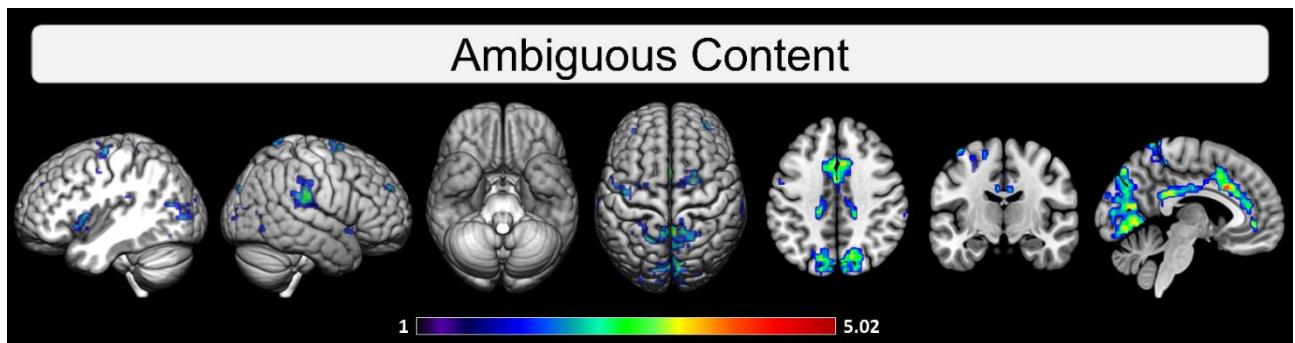


**Figure 5. ATL engagement for semantic, social, and pragmatic content.** A close-up of the lateral (left panel) and inferior (right panel) view of left ATL showing the conjunction of the semantic (green), social (blue), and pragmatic (red) results. Overlap outside of the window outlined in black has been greyed out.

### 3.2.4 Ambiguous content

Listening to sentences with high compared to low ambiguous content was associated with activation in lingual and superior occipital gyri, right middle and superior frontal gyrus, left middle frontal and precentral gyri, right paracentral gyrus, anterior cingulate cortex, bilateral supramarginal gyrus, and bilateral insula (**Figure**

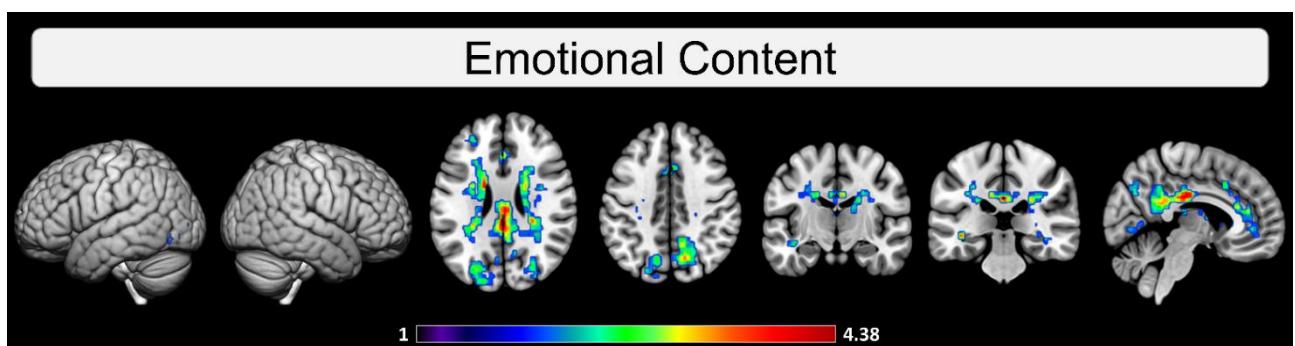
6). The left insular cluster included portions of the inferior frontal gyri: 9.5% of the cluster was the triangularis portion of IFG, 7.8% was the opercularis portion, and 2.2% was the orbitalis portion.



**Figure 6. High > Low ambiguous content results.** Thresholded Z-score statistical map showing lower (purple) to higher (red) values. In order to visualize the left insular cluster that includes portions of inferior frontal gyrus, the left lateral render (far left) has a cut-out along the X-axis ( $x = -56$ ).

### 3.2.5 Emotional content

Listening to sentences with high compared to low emotional content was associated with activation in anterior, middle, and posterior cingulate cortex, precuneus, bilateral middle and superior occipital gyri, right hippocampus and fusiform gyrus (**Figure 7**).



**Figure 7. High > Low emotional content results.** Thresholded Z-score statistical map showing lower (purple) to higher (red) values.

**Table 2***Coordinate Table*

Contrast	Cluster Size	Hem	Brain Region Peak Voxel	Brain Region Highest Overlap [%]	MNI Coordinates		
					X	Y	Z
<i>Semantic High &gt; Semantic Low</i>	23537	L	Heschl's Gyrus	Middle Temporal Gyrus [15%]	-36	-27	14
	4220	R	Heschl's Gyrus	Superior Temporal Gyrus [28%]	40	-23	7
	1976	R	Angular Gyrus	Angular Gyrus [53%]	46	-61	29
	1539	R	Cerebellum (Crus 1)	Cerebellum (Crus 2) [50%]	16	-73	-35
	1426	R	Paracentral Lobule	Paracentral Lobule [33%]	8	-32	66
	1180	L	Precuneus	Precuneus [32%]	-4	-54	12
	1103	L	Rectal Gyrus	Rectal Gyrus [37%]	2	49	-26
	756	R	Middle Orbital Gyrus	Middle Orbital Gyrus [46%]	44	48	-14
	689	R	Fusiform Gyrus	Parahippocampal Gyrus [38%]	26	-32	-21
	492	R	Cerebellum (IX)	Cerebellum (IX) [65%]	4	-53	-58
	293	R	Middle Frontal Gyrus	Inferior Frontal Gyrus (Triangularis) [53%]	46	36	21
	206	R	Precentral Gyrus	Postcentral Gyrus [61%]	48	-24	66
	199	R	Postcentral Gyrus	Postcentral Gyrus [57%]	63	-11	47
	176	L	Precuneus	Hippocampus [32%]	-20	-44	4
<i>Social High &gt; Social Low</i>	2410	L	Superior Medial Gyrus	Superior Medial Gyrus [47%]	-6	56	36
	1838	L	Medial Temporal Pole	Middle Temporal Gyrus [38%]	-51	12	-35
	1250	R	Inferior Occipital Gyrus	Middle Occipital Gyrus [38%]	30	-86	-15
	1141	L	Fusiform Gyrus	Middle Occipital Gyrus [44%]	-36	-82	-14
	1060	L	Precuneus	Precuneus [39%]	-4	-55	28
	982	R	Medial Temporal Pole	Medial Temporal Pole [39%]	48	12	-42
	675	L	Middle Temporal Gyrus	Angular Gyrus [35%]	-53	-55	21
	424	R	Middle Temporal Gyrus	Middle Temporal Gyrus [40%]	48	-22	-11
	271	R	Cerebellum (Crus 2)	Cerebellum (Crus 1) [54%]	26	-81	-48
	226	R	Superior Frontal Gyrus	Superior Frontal Gyrus [51%]	14	39	52
	211	L	Rectal Gyrus	Middle Orbital Gyrus [42%]	-2	61	-16
<i>Pragmatic High &gt; Pragmatic Low</i>	2437	L	Precuneus	Precuneus [34%]	-6	-55	23

	2245	L	Superior Frontal Gyrus	Superior Medial Gyrus [33%]	-14	49	50
	1825	L	Inferior Temporal Gyrus	Middle Temporal Gyrus [64%]	-55	-5	-36
	1575	L	Angular Gyrus	Angular Gyrus [50%]	-53	-62	36
	431	L	Inferior Frontal Gyrus (Orbitalis)	Inferior Frontal Gyrus (Orbitalis) [54%]	-48	34	-22
<hr/>							
<i>Ambiguous High &gt; Ambiguous Low</i>	9996	L	Superior Occipital Gyrus	Lingual Gyrus [11%]	-14	-78	44
	3078	L	Middle Cingulate Gyrus	Precuneus [17%]	-16	-40	50
	2783	R	Superior Frontal Gyrus	Anterior Cingulate Cortex [18%]	20	-1	72
	749	R	Insula Lobe	Insula Lobe [63%]	34	20	8
	723	R	Supramarginal Gyrus	Supramarginal Gyrus [ 57%]	55	-32	29
	623	L	Insula Lobe	Insula Lobe [66%]	-30	27	4
	526	L	Supramarginal Gyrus	Supramarginal Gyrus [62%]	-57	-32	29
	328	R	Middle Frontal Gyrus	Middle Frontal Gyrus [77%]	32	42	33
	285	L	Precentral Gyrus	Precentral Gyrus [38%]	-24	-11	56
	196	L	Precentral Gyrus	Precentral Gyrus [73%]	-40	-14	71
	174	L	Middle Frontal Gyrus	Middle Frontal Gyrus [98%]	-30	40	33
<hr/>							
<i>Emotional High &gt; Emotional Low</i>	10143	R	Middle Cingulate Gyrus	Precuneus [6%]	6	-26	29
	680	R	Anterior Cingulate Cortex	Anterior Cingulate Cortex [34%]	2	28	25
	288	R	Fusiform Gyrus	Hippocampus [27%]	38	-37	-12

Note. Hem, Hemisphere; L, Left; R, Right. Cluster size is determined by the number of 2mm<sup>3</sup> voxels. Highest Overlap [%] is the percent overlap between each result cluster and atlas defined regions (based on the Eickhoff-Zilles macro labels from the N27 (MNI space) atlas). MNI coordinates correspond to the voxel with peak activation within each cluster. Voxels were defined as neighbours based on faces touching (NN=1).

## 4 Discussion

Studies using natural language and narrative stimuli suggest important deviations from the hub-and-spoke neural architecture of the semantic system. Narrative stimuli engage a much broader network alongside the transmodal ventral ATL hub (Deniz et al., 2019; Huth et al., 2012, 2016) and particularly engage dorsolateral ATL (Malik-Moraleda et al., 2022). In conjunction with our other recent studies ([Chapter 3](#); [Chapter 4](#); [Chapter 5](#)), the present results also suggest differences in sensitivity to internally-driven (endogenous) semantic processing within the ATL. In this model, dorsolateral ATL primarily responds to linguistic input whereas ventrolateral ATL is additionally engaged by endogenous semantic processing demands. This claim has implications for how conceptual and inferential social content, which may rely on the semantic and semantic control systems (Balgova et al., 2022; Diveica et al., 2021), is processed during narrative comprehension. The present study quantified several content types, focusing on semantic, social, and pragmatic content, to investigate the extent to which the semantic and semantic control systems are involved in social processing, and whether pragmatic processing, which requires abstract inference that runs counter to the stated word-level meaning of the sentence, engages similar social or semantic brain regions. Results for each content type are discussed in the following sections.

### 4.1 Semantic content

Listening to sentences with high semantic content engaged a broad, bilateral language network, including the transmodal hub in ventral ATL. These results are consistent with prior naturalistic investigations of semantic processing (Deniz et al., 2019; Huth et al., 2012, 2016; Thye et al., 2023; Wu et al., 2022) and with the language comprehension network identified across diverse languages, especially in the left hemisphere (Malik-Moraleda et al., 2022). This convergence validates the sentence-level coding approach adopted here and provides further insight into the naturalistic language processing. The universal language network (Malik-Moraleda et al., 2022) was similarly identified using naturalistic stimuli (i.e., stories) but differed from the current study by using a non-speech baseline condition (i.e., acoustically degraded speech). This isolated regions responsive to language comprehension whereas the current study, by using a baseline condition with coherent language,

identified the bilateral network of regions sensitive to semantic content. Despite this important distinction, both approaches identify approximately the same network, with degree of left superior temporal gyrus engagement being the main difference. Interestingly, the network identified in the present study included a smaller portion of anterior STG (i.e., dorsolateral ATL) than the universal language network. This might suggest that portions of STG are sensitive to quantity of linguistic input (which was statistically controlled in the high-versus-low semantic contrast) whereas other portions are additionally sensitive to semantic input specifically.

Although the results are broadly consistent with a hub-and-spoke architecture and the role of ATL as a graded hub (Lambon Ralph et al., 2017), they suggest that naturalistic semantic processing engages a much broader network than was inferred from studies using experimental manipulations derived from non-naturalistic stimuli. In addition to engagement of the ventral ATL hub in anterior fusiform gyrus, dorsolateral and (to a much lesser extent) the anterior portion of MTG in ventrolateral ATL were engaged by sentences with high semantic content (**Figure 5**). This is consistent with other recent studies of naturalistic story comprehension (Malik-Moraleda et al., 2022)([Chapter 5](#)) and with the distinction between processing semantic input versus endogenous semantic processing. That is, dorsolateral ATL may be particularly sensitive to quantity or informativeness of semantic input, which is why it is identified in the universal language network and the present study, whereas ventrolateral ATL (i.e., anterior portions of MTG and ITG), which is less robustly identified in either network, is also engaged for endogenous semantic processing such as updating the situation model of the overall narrative. As a result, ventrolateral ATL is active for both high and low semantic *input* sentences, though it is engaged in somewhat different semantic processes: during high semantic input sentences it is engaged in processing that input, during low semantic input sentences it remains active but is engaged in endogenous semantic processing. The engagement of the ventrolateral ATL is then approximately, but not exactly, matched between the high and low semantic contrast. When stimuli are presented in a random order without a narrative context (i.e., typical lexical semantics experiments), this region is consistently more active in the semantic condition because there is no endogenous semantic processing to engage it during the low/non-semantic condition.

## 4.2 Social content

Highly social content engaged bilateral ATL, in particular both the ventrolateral and dorsolateral portions of left ATL, but not the hub in ventral ATL. The ATL results partially overlap with the semantic content results, though, in MTG, the semantic content effects were more posterior than the social content effects, and a larger portion of dorsolateral ATL was engaged for social compared to semantic content (**Figure 5**). Critically, engagement of ventrolateral ATL was observed despite matching the quantity of semantic content in the high and low social conditions. This is consistent with the claim that social knowledge, like other types of semantic information, is processed within ventrolateral ATL (Balgova et al., 2022; Binney & Ramsey, 2020) and provides critical converging evidence in support of this claim by observing the same pattern during naturalistic social processing. We did not observe engagement of the ventral ATL hub, however, suggesting that there are functional differences between the ventral and ventrolateral ATL, consistent with the graded hub account (Lambon Ralph et al., 2017).

Sensitivity within the semantic system for social processing may indicate that a social semantic network exists alongside the sensory-motor semantic network (Lin et al., 2018; Zhang et al., 2021). In this view, the social semantic network displays two key features: (1) sensitivity to social information and (2) sensitivity to the accumulation of semantic information which may be particularly relevant for social processing. Indeed, activation in both ATL and TPJ increases as the constituent size of sentences increases, reflecting semantic accumulation (Pallier et al., 2011), but also when the social and emotional content increases (Mellem et al., 2016). Critically, the semantic accumulation effect appears most strongly in dorsolateral ATL, in line with the claim that this region is sensitive to the external semantic processing driven by the quantity of input. In a prior study examining processing of words, sentences, and passages that were given subjective social ratings, dorsolateral ATL was consistently engaged by high relative to low social content across all linguistic hierarchies whereas dorsomedial prefrontal cortex, precuneus, and bilateral TPJ were engaged only for highly social sentences and passages (Zhang et al., 2021). These results broadly align with the results of the present study, but we provide an alternative interpretation. Engagement of ATL, in particular the dorsolateral subregion, across linguistic hierarchies and in response to increases in

social content ratings is consistent with the graded hub account. Activation in this region but also the ventrolateral region is observed in the present study, and social concepts relative to matched non-social concepts have been shown to similarly engage ventrolateral but not dorsolateral ATL (Binney et al., 2016). Further, unlike the current study, Zhang et al. only rated social content and was thus not able to match the high and low conditions on semantic, or other, content types. In addition, sentences or shorter passages were used instead of a protracted narrative. According to the endogenous semantic processing account, social content provided with minimal context may not drive endogenous processing and, thus engage ventrolateral ATL, to the same extent as the same information presented in context, requiring integration into a much more elaborated situation model. We argue that the results suggest that ventrolateral ATL is particularly sensitive to internal or endogenous semantic processing during narrative comprehension, and that social content is processed with the semantic system.

There was also evidence of engagement of regions more commonly associated with social cognitive processing, such as prefrontal regions and precuneus (Adolphs, 2001, 2009). Activation in right supramarginal and angular gyri (i.e., TPJ) was notably absent. This region may be specifically sensitive to theory of mind processing, which was not explicitly manipulated in the present study (Saxe & Kanwisher, 2003). However, portions of the social cognition network, in particular medial frontal regions, are engaged during narrative comprehension more generally, even in the absence of social content (Jacoby & Fedorenko, 2020). Narrative processing is also known to engage precuneus, possibly due to the longer temporal receptive window of this region (Hasson et al., 2008; Xu et al., 2005). In the current study, highly semantic content was associated with activation in precuneus, although it was engaged to a greater extent by social and pragmatic content, consistent with the role of this region in social processing (Adolphs, 2009). Alternatively, activation in precuneus and other default mode network regions (i.e., posterior cingulate, dorsomedial prefrontal cortex) may evidence the connections between ventrolateral ATL and the DMN that facilitate endogenous semantic processing.

### *4.3 Pragmatic content*

Pragmatic and social content engaged a similar network of regions, which may be because pragmatic inference requires social cognition about the narrator's or character's intentions and mental states (Levinson, 1983). However, the overlap did not occur in the core theory of mind region within right TPJ. In addition, processing of highly pragmatic narrative content was left lateralized, despite some evidence that right hemisphere regions play a greater role in pragmatic processing (Cutica et al., 2006). Importantly, social and pragmatic content ratings were not merely proxies of each other. The ratings did not identify the same set of sentences, although some sentences were both highly social and highly pragmatic. Social content was matched between the high and low pragmatic sentences, and pragmatic content was matched between the high and low social sentences. In other words, the comparison is analogous to a 2x2 factorial experiment that independently manipulated social and pragmatic content, but these sentences were presented in the context of one protracted narrative.

Interestingly, both social and pragmatic content engaged the ventrolateral ATL. Although not a region consistently implicated in pragmatic processing (Tomasello, 2023), a prior study using passive processing of indirect versus direct statements in dialogues similarly reported engagement of the same ventrolateral portion of ATL (Bendtz et al., 2022). This may suggest that the semantic system is engaged for abstract, inferential socio-cognitive processing, a claim that has been empirically supported using non-verbal social cognition tasks (Balgova et al., 2022). In line with this account, we observe engagement of this ventrolateral region for highly social narrative content, but observing the same engagement for pragmatic content provides compelling evidence that the semantic system is encoding both representational and inferential social knowledge. In other words, the semantic system is not only engaged for processing social concepts, but appears to also be engaged when processing abstract social information that is not simply in the words comprising the sentence.

Pragmatic inference requires using narrative context to reach a non-literal interpretation of the input, which is a type of endogenous semantic processing. Thus, these results provide support for the claim that endogenous semantic processing engages ventrolateral ATL, and not dorsolateral ATL which was minimally active

here. An alternative explanation is that ventrolateral ATL may be particularly sensitive to pragmatic and/or social content, but evidence in support of this claim is inconsistent (Binney et al., 2016; Zahn et al., 2007) and runs counter to the empirical support for its role in domain-general semantic processing (Balgova et al., 2022; Binney et al., 2010; Lambon Ralph et al., 2017).

Instead, the narrative content may drive endogenous semantic processing demands. Social and pragmatic content is particularly important to the narrative used here. The interactions between the narrator and the little prince or between the little prince and the inhabitants of the planets he visits provide the critical plot-progressing information that requires updating situation models. The processing of pragmatic inference is also likely to require significant internal semantic processing – the listener must reflect on the mental states of the agents in the scene and situate the information in context, recalling the relevant preceding information. In line with the endogenous semantic processing framework, this may explain why the ventrolateral ATL, in particular anterior MTG, is robustly engaged across the social and pragmatic results, whereas dorsolateral ATL is minimally engaged by pragmatic content (**Figure 5**). Centering of social content is common in narratives, but not universal; narratives that oversample a very different kind of content may drive engagement of the ventrolateral region in different ways. Take, for instance, a mystery novel in which the factual information and details required to problem solve and anticipate the outcome are more critical to the plot and overall understanding of the context. In this case, these details, rather than the social content, may drive engagement of ventrolateral ATL to a greater extent than the social content which does not enable a resolution of the plot tension.

In reconciling the current results with prior research on neuropragmatics, it is important to consider the type of pragmatic inferences captured with subjective sentence content ratings. As an example, consider the widely studied case of scalar implicatures (Noveck & Reboul, 2008) – whether a word like “some”, which could logically include the case of “all”, is taken to include that meaning or not. Such underspecified scalar terms do occur in the narrative, for example in “Now there were some terrible seeds on the planet of the little prince, there were the seeds of baobab trees.” The listener would likely assume (pragmatically infer) that not all of the seeds on the little prince’s planet were terrible (nor that all terrible seeds were

only on the little prince's planet). However, this sentence received a low pragmatic content rating because the subjective sense of making a pragmatic inference is much stronger for conversational implicatures in which a character responds to the implied meaning of the speaker (Grice, 1989). An interaction between the king and the little prince demonstrates this well:

*"Yes," said the little prince, "but I can judge myself anywhere, I do not have to live here."*

*"Hum! Hum!" said the king. "I am fairly certain that somewhere on my planet there is an old rat."*

On the surface, knowledge of a rat inhabitant is not relevant to the exchange unless we understand the king's inference that the little prince is asking for someone to judge and the king's intention to have the prince judge this rat. This sentence received a high pragmatic content rating.

In addition to conversational implicatures, the content ratings identified other routinely studied pragmatic phenomena: verbal irony and sarcasm. Ironic utterances are those in which the meaning is the opposite of what is said, such as when the narrator, having received harsh appraisal for several bad drawings, says, *"Thus, I abandoned at the age of six a magnificent career as a painter."* Sarcasm is a type of verbal irony but is used to criticize or condemn the actions of another, such as when the narrator, judging the close-mindedness of the grown-ups, says, *"and the grownup was glad to know such a sensible man."* Understanding an ironic or sarcastic utterance requires inferring the mental state and intention of the speaker (Wilson, 2006, 2009). Neither of these examples would be correctly interpreted at face value without prior knowledge of the narrator's experiences and attitudes and, as a result, received high pragmatic content ratings. This is an important point of intersection between the current naturalistic work and prior studies of pragmatic processing that used more simplified stimuli. The subjective pragmatic content ratings captured conversational implicatures and non-literal language of the same type and form as those manipulated in non-narrative stimuli (Blome-Tillmann, 2013).

Interestingly, the results overlap with the network observed for processing non-literal compared to literal language (Bohrn et al., 2012; Hauptman et al., 2023; Reyes-Aguilar et al., 2018). Comprehension of non-literal language is not wholly

separable from pragmatic processing, although the former does not inherently require socio-cognitive processing. Some types of non-literal language, such as irony and sarcasm discussed above, do require pragmatic inference and are studied independently as pragmatic phenomena (Wilson, 2006, 2009). Activation in left superior frontal gyrus, inferior frontal gyrus, inferior parietal lobule, and precuneus is consistent with the network of regions that support processing of verbal irony and sarcasm (Obert et al., 2016; Spotorno et al., 2012), and aligns with the lack of right hemisphere lateralization broadly observed in meta-analyses of non-literal language processing (Bohrn et al., 2012; Hauptman et al., 2023; Reyes-Aguilar et al., 2018). Recruitment of left IFG for pragmatic inferences as well as for non-literal language that is not social (e.g., metaphors) may be driven by the general role of IFG in incongruity detection and resolution (Whitney et al., 2012). The present results suggest that processing these pragmatic phenomena engages similar brain regions to processing other kinds of strongly social interaction content.

#### *4.4 Ambiguous content*

Highly ambiguous sentences engaged only a small portion of left IFG and none of pMTG, which suggests only partial engagement of the semantic control system. Instead, activation was seen in bilateral insula, anterior cingulate cortex, small frontal clusters (right paracentral gyri, middle and superior frontal gyri), bilateral supramarginal gyri, and superior occipital gyrus. This result is only partially consistent with the predictions derived from an established body of research on sentence-level ambiguity resolution. We suggest this may be due to several possible factors.

First, with only 46 highly ambiguous sentences, the analysis may have been underpowered. Even so, we might anticipate that the strongest statistical association would be present in left IFG due to the role of this region in ambiguity resolution and control demands more generally (Jackson, 2021; Rodd et al., 2010, 2010), but the peak voxel of the left IFG cluster was in the insula. Second, ambiguity was defined coarsely as difficult-to-understand sentences, which included (1) syntactic ambiguity, (2) semantic ambiguity, and (3) narrative ambiguity. Manipulating syntactic and semantic ambiguity at the sentence level is an established approach for studying ambiguity resolution, so the incorporation of these definitions was motivated by this

prior work (Rodd et al., 2010). It is unclear, however, how people resolve narrative ambiguities, and it is also less straightforward to measure. This definition was included after discussions while coding the practice narratives because it became evident that narratives frequently present confusing, indefinite information that results in a subjective awareness of ambiguity. Incorporation of this third type of ambiguity alongside more traditionally studied sources of sentence-level ambiguity is consistent with theories of semantic control and ambiguity resolution (Jackson, 2021; Lambon Ralph et al., 2017; Vitello & Rodd, 2015). These theories make reference to general mechanisms such as inhibition of irrelevant information, selection among competing alternatives, and controlled retrieval, all of which are required in the narrative ambiguity case. Third, narrative ambiguity was more common than syntactic or semantic ambiguity, which is unsurprising given that narratives, especially those written for children, would tend to avoid complex or confusing language. As a result, the ambiguity contrast minimally captured syntactic and semantic ambiguity.

Consider the following sentence from the narrative: “*That is right, and if you are good I will give you a rope to tie him up with during the day and a stake.*” The word “stake” is a homophone because it sounds like the word “steak” but means something different. Hearing (and not seeing) that word requires resolving competition between the different interpretations; however, in context, the sentence was readily understood and rated as low ambiguity. Consider instead this example: “*It was in this way that on the third day, I came to know of the tragedy of the baobabs.*” This sentence was given a high ambiguity rating because it is not clear why baobabs, a seemingly innocuous tree, were tragic. This sentence was presented with minimal preceding information to aid in disambiguating the meaning. These narrative moments are what readers find subjectively ambiguous in narratives. The subjective awareness of the need to resolve ambiguity in narratives is thus capturing something quite different than previous studies of ambiguity resolution.

#### 4.5 Emotional content

There was evidence of engagement of the limbic system (cingulate cortex, right hippocampus, thalamus) when listening to highly emotional content in a narrative,

which aligns with prior research and is consistent with the role this system plays in processing emotion (Barson et al., 2020; Palomero-Gallagher & Amunts, 2022; Rolls, 2019). Activation in amygdala was notably absent, however. We also did not observe a right hemisphere bias in processing emotional narrative content.

There are several possible explanations for why our results diverge from research on emotion processing in this regard. First, emotion processing may be highly dependent on context. Tasks such as reading isolated emotion words or seeing static images of (often exaggerated) facial expressions may artificially constrain emotional experience compared to naturalistic stimuli that evoke a more complex emotional experience. As a result, context-free stereotyped emotion stimuli may engage brain networks that differ substantially from those engaged when emotions are experienced during narrative comprehension or natural language processing (Saarimäki, 2021).

Second, social and emotional content were confounded: highly emotional sentences also tended to be highly social. As a result, social content could not be subtracted from the emotion analysis. We suspect that this is a prevalent issue outside the present work given that social content is rarely considered in studies of emotional content in sentences and passages (e.g., Bestgen, 1992; Hsu et al., 2015). Narratives may also oversample social content, resulting in relatively few emotional moments that occur outside of a social context. Despite this, the emotion content results isolated a distinct network from the social content results, suggesting that the content types were not merely capturing the same underlying narrative or cognitive property.

Third, our emotion ratings, like all the content ratings, were made one sentence at a time, as the rater listened to the narrative. The interruptions to record sentence ratings may reduce the emotional impact of the sentences and events by taking the rater out of the moment. Highly emotional moments may thus have been coded as only moderately emotional and excluded from analysis. The categorical coding approach partially provides a buffer against this problem, however. The differences between low versus moderate and moderate versus high are easier to distinguish than numeric ratings, which are more impacted by idiosyncratic differences in perception and experience of the narrative. A related consideration is that emotional reactions to narrative content may be more subjective or variable across people than

the other content types examined in this study. This highlights the challenge of selecting context-free stimuli and tasks that generalize to naturalistic processing (Yarkoni, 2022).

## 5 Conclusion

The results of the present study suggest that social processing is supported by the semantic system, particularly ventrolateral ATL, and that functional subregions within ATL support different aspects of narrative comprehension. During natural language or narrative processing, ventrolateral ATL is engaged by internally-driven semantic processing demands. Sentences with high semantic (i.e., informative) content engaged the ventral ATL hub and dorsolateral ATL more than less informative sentences did. Highly social and highly pragmatic sentences, matched on semantic input demands, engaged ventrolateral ATL and not the ventral ATL hub. We argue that this is due to the importance of social and pragmatic content in progressing the narrative plot; that is, engagement in endogenous semantic processing. Although the present data are consistent with an alternative account that ventrolateral ATL is specialized for social processing, this would be inconsistent with extensive evidence of the role of ventrolateral ATL in domain-general semantic processing. The functional role of ventrolateral ATL may have been missed in prior single word or sentence-level studies of semantic cognition because they present stimuli in a random order with minimal context, which minimizes endogenous semantic processing. Taken together, this study indicates that social processing, including abstract pragmatic inference, is supported by ventrolateral ATL in naturalistic contexts.

# **Chapter 5**

## **THE NEURAL BASIS OF NATURALISTIC SEMANTIC AND SOCIAL COGNITION**

### **Abstract**

Decoding social environments and engaging meaningfully with other people are critical aspects of human cognition. Multiple cognitive systems, including social and semantic cognition, work alongside each other to support these processes. This study investigated shared processing between social and semantic systems using neuroimaging data collected during movie-viewing, which captures the multimodal environment in which social knowledge is exchanged. Semantic and social content from movie events (event-level) and movie transcripts (word-level) were used in parametric modulation analyses to test (1) the degree to which semantic and social information is processed within each respective network and (2) engagement of the same cross-network regions or the same domain-general hub located within the semantic network during semantic and social processing, which would indicate integration between the social and semantic cognitive systems. This reveals the neural basis of social and semantic cognition during naturalistic processing.

## 1 Introduction

Social knowledge is a fundamental aspect of human cognition: it informs our moment-by-moment understanding of our social world, and it directly motivates human behaviour (Adolphs, 2009). Through our understanding of social concepts and behaviours we are able to effectively and accurately communicate complex, abstract ideas and participate in meaningful interpersonal interactions. Many of these processes are, at least partially, supported by the social cognition system, which is broadly engaged in integrating and updating information about the actions, beliefs, motives, and mental states of ourselves and the people in our environment. Much of the research on social knowledge has focused on characterizing how individuals engage the social cognition system to process information about their own and others' actions and perspectives (Beaudoin & Beauchamp, 2020).

Decoding and reciprocating interactional dynamics leverages a whole host of other cognitive systems, ranging from perceptual and attentional systems to higher-order language and executive systems (Adolphs, 2001). Shifting from a strict domain specificity approach and adopting models from other domains of cognition may result in greater insights in social neuroscience (Ramsey & Ward, 2020; Spunt & Adolphs, 2017). One key contributor is semantic cognition, which allows us to know and communicate about both the linguistic and non-linguistic physical and emotional properties of the objects, people, and events we experience, and gives meaning to the language we use (Binney & Ramsey, 2020; McRae & Jones, 2013; Rice et al., 2018; Tulving, 1972). The breadth and complexity of social knowledge requires mutual or interacting support from both social and semantic cognition, and the present study examines the degree to which social cognitive processing leverages the neural architecture of the semantic system.

A rich history of research on pragmatics shows that social cognition plays an important role in communication, where context and non-linguistic features convey critical information that is not present in the lexical units or syntactic structures themselves. This pragmatic content allows comprehension of the intended meaning beyond the surface linguistic content (Bambini, 2010; Hagoort & Levinson, 2014) and requires the social cognitive process of mentalizing about the perspectives of the other agents in the environment (Levinson, 2006). Retrieval of the relevant social knowledge - from the names and behaviours of the people we encounter to the

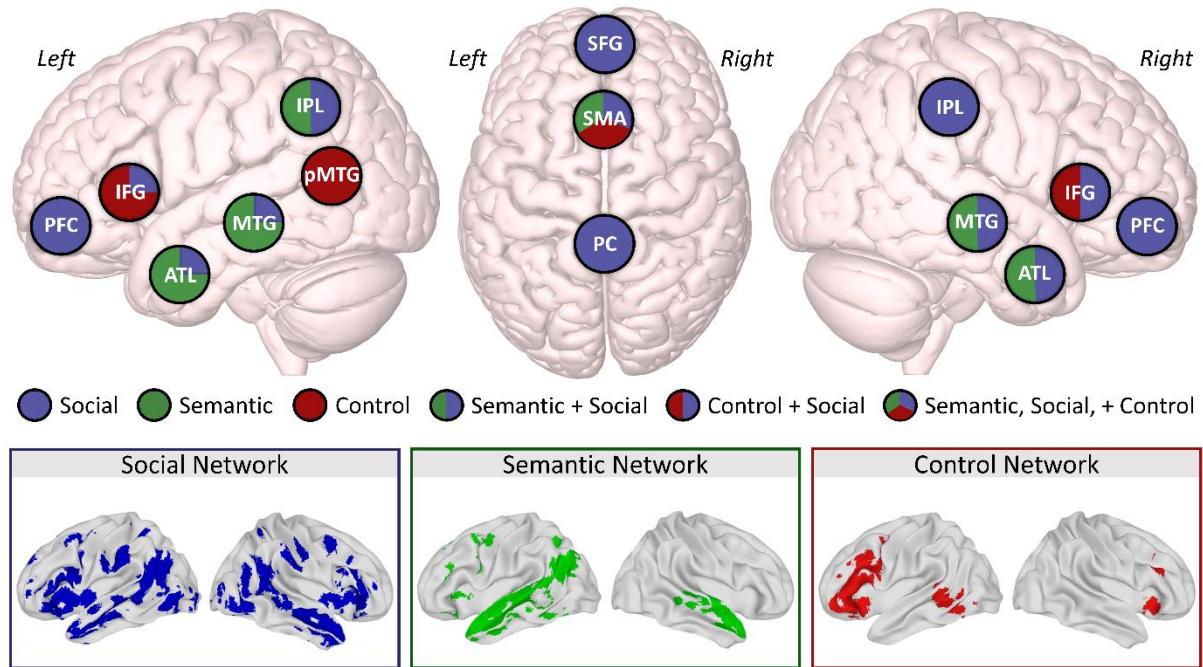
concepts used to label those behaviours - may rely on semantic memory, which is an acquired conceptual store of linguistic and non-linguistic information about the multimodal world around us, informed by interactions with new objects, events, experiences, and people (Binney & Ramsey, 2020; McRae & Jones, 2013; Ross & Olson, 2010). Although pragmatics is predominately concerned with how communicative intent is inferred in the presence or absence of linguistic input which is separate from the goals of the present study, the research in this domain emphasizes the importance of the social cognition system in communication, a role which is also facilitated by semantic memory.

One clear point of intersection between semantic and social cognition is the representation and processing of social concepts. What makes these concepts ‘social’ is their use in ascribing meaning to human behaviour, intentions, desires, feelings, and interactions (Zahn et al., 2007). This type of social knowledge is often (although not universally (Diveica et al., 2023)) described as intangible or abstract, not grounded in sensory or perceptual representations (Hoffman, 2016). Current neurocomputational theories posit that abstract semantic representations arise through statistical regularities in the contexts in which they occur, especially natural language contexts. Concepts such as *jealousy* and *ambition* co-occur with concrete concepts in specific contexts, and knowledge about our own and others’ emotions, intentions, and beliefs is encoded along with the environment in which they occurred, thus giving rise to abstract social concepts (Barsalou, 2020; Borghi & Binkofski, 2014; Hoffman et al., 2018). Social concepts, like other types of semantic knowledge (Binney et al., 2016; Zahn et al., 2007), are acquired through interactions in social environments in which individuals display or communicate about the behaviours associated with these concepts. As a result, these concepts are predominately not understood through sensory systems, and are instead directly informed by and grounded in emotion (Vigliocco et al., 2014), introspection (Shea, 2018), and social experiences (Borghi & Binkofski, 2014). The roles of semantic and social cognition in acquiring social knowledge are thus inseparable.

In addition to shared conceptual knowledge, the semantic and social systems are supported by an overlapping network of brain regions (**Figure 1**) (Adolphs, 2001; Binney & Ramsey, 2020; Patterson et al., 2007). This overlap predominately occurs in the anterior temporal lobes (ATL) and the left inferior parietal lobule, regions which

are consistently reported in semantic processing (Lambon Ralph et al., 2017; Xu et al., 2018), including representing and retrieving social knowledge (Binney et al., 2010; Olson et al., 2013; Zahn et al., 2007), and in mentalizing tasks (Frith & Frith, 2006; Monticelli et al., 2021). Engagement of the same regions for semantic and social processing has motivated a theoretical account, the *graded semantic hub hypothesis*, which argues that social cognition requires semantic memory and the neural architecture of the semantic cognition and semantic control systems (Balgova et al., 2022; Binney et al., 2016; Binney & Ramsey, 2020). The same ventrolateral portion of left ATL is engaged by theory of mind processing and non-verbal semantic processing (Balgova et al., 2022), and a recent meta-analysis found that both cognitive systems rely on a shared cognitive control network (Diveica et al., 2021), which provides empirical support for this account. In addition, the ATL may be ideally positioned to serve as a hub for processing both semantic and social information given the structural connections of the uncinate fasciculus projecting from ATL to emotion processing areas in amygdala and orbitofrontal cortex (Olson et al., 2013). Notwithstanding this evidence of overlap, there is also extensive evidence that the networks that support language processing and theory of mind processing are separable (Fedorenko & Varley, 2016; Paunov et al., 2022). Compelling evidence of this dissociation comes from lesion studies in which individuals with extensive left hemisphere damage or aphasia have preserved theory of mind processing or ability to comprehend communicative intent (Goodwin, 2006; Varley & Siegal, 2000). This dissociation is not observed in patients with semantic dementia, which is characterized by bilateral ATL damage, who display impairments in both semantic and social processing (Duval et al., 2012). This suggests that the location of the damage (i.e., whether the damage occurs in a shared ATL processing hub) may determine whether only one or both systems are affected. There is thus ample evidence that language and social processing can be dissociated, but a focus on separability ignores potential insights about interactive processing (Patterson & Plaut, 2009; Schwartz & Dell, 2010) and cannot answer whether the regions engaged by both systems are responding to both types of content (i.e., semantic and social processing) or serving as domain-general hubs that support both processes. In this view, specialization, and therefore dissociation, does occur for semantic and social processing which separately recruit more specialized regions outside of these hubs.

Overlapping neural networks may simply indicate that the semantic and social systems work alongside each other, with areas of overlap performing separate functions within each system (no shared processing) or there may be non-overlapping specialized subregions for processing semantic or social information (graded functioning). Alternatively, domain-general areas may perform the same function within each system (shared processing) or a known semantic or social hub may integrate information to facilitate processing both semantic and social information (shared hub). One reason to expect shared processing or a shared hub is that semantic and social cognition have been proposed to consist of analogous representation and control processes. Control processes for both systems are supported by a shared control network (Diveica et al., 2021), and the hub-and-spoke sensorimotor architecture of the semantic representation system lends itself well to multimodal social perceptual stimuli (Binney & Ramsey, 2020). Recent research provides critical evidence in support of this claim (Balgova et al., 2022), but the social and semantic tasks used were highly simplified and thus impoverished approximations of real-world cognition. Also, the inferences were drawn from the group-level statistical map rather than overlap at the individual participant level. Stronger evidence of shared processing or a shared hub would come from using naturalistic paradigms and investigating the neural overlap of these systems within individuals because idiosyncratic variations in neuroanatomy and functioning are ignored when aggregating results at the group-level (Fedorenko & Kanwisher, 2009). The latter is especially relevant when studying regions that may have graded functioning. Previous research attempting to isolate theory of mind (i.e., false belief) and linguistic (non-social stories) processing within the superior temporal sulcus (STS) found overlapping voxels in both posterior and anterior portions of STS that responded to both types of content within individuals (Deen et al., 2015). These results suggest that the neural overlap reported in group studies is capturing meaningful overlap that exists within subjects, but did not test broader semantic and social systems. The present study investigated whether there is evidence of shared processing in domain-general regions or within a shared hub in ATL that support both systems at the individual and group level in the same naturalistic context.



**Figure 1. Social, semantic, and semantic control brain networks.** A schematic showing the critical regions within the social network (blue), semantic network (green), and semantic control network (red) is shown in the top panel. The overlap between the regions within each network is indicated by circles with mixed colours, and the relative extent of overlap is shown by the amount of colour associated with a given network in each circle (either approximately equally shared – indicated with  $\frac{1}{2}$ - $\frac{1}{2}$  shading – or predominately reported for one system with a smaller subset of the region reported for the other system – indicated with  $\frac{3}{4}$ - $\frac{1}{4}$  shading). The statistical maps derived from coordinate-based activation likelihood estimation (ALE) analyses of social cognition (Diveica et al., 2021) and semantic cognition and semantic control (Jackson, 2021) are shown in the bottom panel. ATL, anterior temporal lobe; IFG, inferior frontal gyrus; IPL, inferior parietal lobule; MTG, middle temporal gyrus; PC, precuneus; PFC, prefrontal cortex; pMTG, posterior middle temporal gyrus; SFG, superior frontal gyrus; SMA, supplementary motor area.

For tractability, researchers tend to fractionate human cognition into modules and study these modules as independent, non-overlapping systems (Binney & Ramsey, 2020). A prevalent, perhaps unintentional, example of this treatment of cognition can be seen in standard fMRI contrast analyses in which a cognitive process of interest is isolated by measuring an experimental condition (i.e., social communication) and subtracting from it a control condition that minimally requires the cognitive process of

interest (i.e., non-social communication). Studies utilizing this methodology have generated significant insights into many aspects of human cognition, including both social and semantic cognition. This methodology assumes an additive relationship between the processes such that it can be undone by subtraction (i.e., control processes operate in the same way in the control and experimental conditions). Although this assumption may be approximately valid in many cases, it explicitly does not hold for integrated or interactive systems. Subtracting non-social communication from social communication to identify “social cognition” assumes that communication works the same way in social and non-social contexts (e.g., no social knowledge is nested within the subtracted semantic system, which conflicts with existing evidence (Binney & Ramsey, 2020)) and that social cognition works the same way in communication and non-communication contexts (i.e., subtracting the communication component leaves task-independent social cognition that would operate similarly in non-communication contexts). This research strategy has led to the impression that all cognitive systems are subtractable and independent in the mind and brain, rather than just being separate in the research literature.

In addition to this general treatment of human cognition, the relationship between these two cognitive systems has been obscured by differences in the types of paradigms used to study them. Studies have tended to rely on highly simplified experiments to investigate both semantic and social processing, but there is greater diversity in the content and presentation of paradigms used to study social cognition. Semantic tasks often involve single words or pictures, whereas the stimuli used in social tasks range from single word and sentence stimuli to face stimuli and social animations. As a result, the same social cognitive process (e.g., mentalizing) can be elicited by heterogeneous tasks (e.g., false-belief vignettes, comic strips, strategic games, animations) which complicates cross-task inferences due to varied task demands (Kliemann & Adolphs, 2018; Schaafsma et al., 2015). These methodological differences hinder investigations of shared processing between semantic and social cognition due to the challenge of identifying stimuli and paradigms with matched processing demands that meaningfully capture both systems. This would ideally be accomplished by eliciting semantic and social processing within the same paradigm.

Given the specific barriers that have hindered investigations of the interdependence between semantic and social cognition, it is critical to select stimuli that adequately capture varied social knowledge, including social semantic information (i.e., social concepts) and social interaction information (i.e., social events). An ideal avenue to accomplish these complementary goals is through the analysis of naturalistic neuroimaging data. Naturalistic neuroimaging provides greater ecological validity compared to studies of isolated word processing, which do not capture how the brain processes information in the real-world and disregards the context that informed the conceptual representation (Redcay & Moraczewski, 2019; Sonkusare et al., 2019; Zaki & Ochsner, 2009). Social information occurs in dynamic and multimodal contexts in which knowledge accrues over several seconds to minutes, which naturalistic paradigms more closely approximate. One type of naturalistic paradigm, movie viewing, has been shown to produce stable intrinsic connectivity networks that are more reliable than those derived from resting state data (Finn et al., 2017; Vanderwal et al., 2017) and which provides the opportunity to capture temporal structure that would be lost in a traditional event-averaging fMRI analysis (Ben-Yakov et al., 2012). Further, humans segment continuous experiences into discrete events (Baldassano et al., 2017) and cortical regions have varied temporal receptive windows that are directly impacted by the duration and content of these events (Hasson et al., 2008; Lerner et al., 2011). Naturalistic paradigms allow for the investigation of both short (i.e., 1000ms) and long temporal processing across cortical regions in response to varied content.

The aim of the present study was to investigate the shared and distinct neural organization of social, semantic, and semantic control brain networks by examining the response of these networks to semantic and social information in movies, while distinguishing between word-level and event-level representations. The study utilized the publicly available Naturalistic Neuroimaging Database (NNDb), which includes hours of movie viewing fMRI data for a large sample of adults (N=86) (Aliko et al., 2020). Of note, the data include 10 different movies, which enables tests of generalizability of results across stimuli and provides an opportunity to sample varied social concepts and events. Independent ratings of semantic and social content from manually coded events for each movie were used as continuous event-level variables. Lexical and semantic content and smoothed factor scores indexing

Semantic Flexibility and Social Impact were used as continuous word-level variables. The continuous variables were used to identify regions of the brain that respond to semantic and social content and to examine the degree that neural resources are shared between the systems at the individual and group level. The primary aims and predictions of the current study are divided into two complementary research questions (the pre-registered design table is [Appendix D: Supplemental Table 1](#)).

First, during naturalistic movie viewing, is semantic, social, and semantically flexible (i.e., having several uses or meanings) content associated with increased activation in the semantic, social, and semantic control networks, respectively? It was expected that clusters of voxels showing increased activation in response to greater semantic, social, and semantically flexible word-level content will fall within the semantic (hypothesis 1.1a), social (hypothesis 1.1b), and semantic control (hypothesis 1.1c) brain networks, respectively. Further, it was expected that the clusters of voxels associated with semantic and social event-level content will fall within the semantic (hypothesis 1.2a) and social (hypothesis 1.2b) brain networks, respectively.

Second, to what extent are the semantic and semantic control networks involved in processing social concepts and events in individual subjects? If there are clusters of voxels that respond to social word-level and event-level content, then it was expected that both social concepts and social events will engage areas of overlap within the semantic (hypothesis 2.1a) and semantic control (hypothesis 2.1b) brain networks defined within individual participants. This would provide evidence of shared resources between the social and semantic systems. If that overlap occurs within the known semantic hub, ATL, this will provide support for the *graded semantic hub* hypothesis, suggesting that the systems leverage a shared hub. In addition to overlap, it was expected that non-overlapping, proximal clusters of voxels will differentially respond to semantic and social content (hypothesis 2.2a) and semantic control and social content (hypothesis 2.2b), providing evidence of graded functioning within network regions.

## **2 Methods**

### *2.1 Ethics information*

The research complies with all relevant ethical regulations. The project from which the data are derived was approved by the ethics committee of University College London. Participants provided written informed consent to take part in the study and have their anonymised data shared.

### *2.2 Design*

The research questions were tested via secondary analyses of a publicly available dataset called the Naturalistic Neuroimaging Database (NNDb) which is accessible on OpenNeuro ([https://openneuro.org/datasets/ds002837/VERSIONS/2.0.0](https://openneuro.org/datasets/ds002837 VERSIONS/2.0.0)). Version 2.0.0 of the database (released April 20, 2021) was used for all analyses and includes the raw and preprocessed data from 86 participants (mean age = 26.81; 42 females) who watched one of ten movies (length range = 5470 - 8882s) while undergoing fMRI. Movie selection was decided by previous exposure, so all participants were shown a movie they had not previously watched. At least 6 and up to 20 participants watched each movie.

None of the authors had previously analysed the participant data from any version of this dataset nor had any direct knowledge of the data at the time of pre-registration. All analyses were registered prior to any human observation of the neuroimaging data. The movie annotation files were obtained prior to registration and coded using protocols designed to (1) segment the movies into discrete events and (2) derive a range of continuous variables encoding the presence of word and event-level semantic and social information at each point in time (see below). For a detailed overview of the experimental procedures, including how the data were collected and preprocessed, see the publication describing the dataset (Aliko et al., 2020).

### *2.3 Sampling plan*

The current study is a secondary analysis of existing data, and, as such, the sample size is fixed. With 86 participants who each watched a full feature-length film,

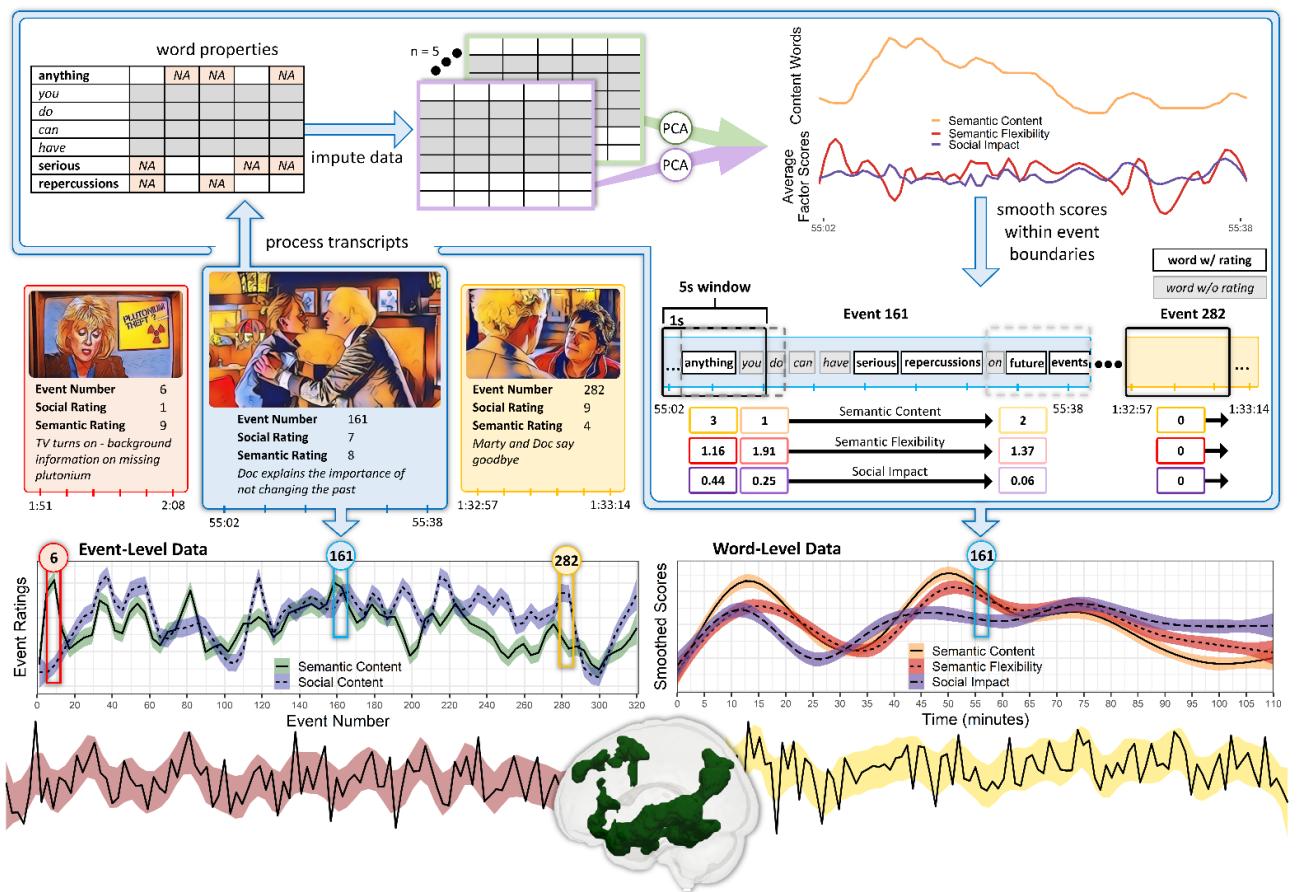
the NNDb is among the largest publicly available databases of naturalistic neuroimaging data to date (though see the *Narratives* dataset (Nastase et al., 2021)), and currently the largest dataset that uses movie stimuli. Comparable databases often have fewer than 30 participants, and many use stimuli that are less coherent (i.e., clips of adverts or scenes from films) or shorter in duration (i.e., single episodes or short films). Task-based fMRI studies require more than 80 participants to detect medium effect sizes (see power analysis below) (Geuter et al., 2018), and scan times greater than 90 minutes produce more reliable results (Gordon et al., 2017). With the large sample size and the longer scan duration, the NNDb provides more data per participant than many other naturalistic neuroimaging databases.

A sensitivity power analysis was conducted using the *pwr* package in R (Champely, 2020) to determine what effect size is detectable given the fixed sample size. This type of power analysis is a complement to the more common *a priori* power analysis which assumes an effect size and computes the sample size necessary to detect that effect. With the fixed sample size of 86, statistical power of .95, and an alpha of 0.05, an omnibus multiple regression analysis with 2 to 3 predictors would be sensitive to detecting medium effects ( $f^2 = 0.19\text{--}0.21$ ). This is a conservative estimate of statistical power because it does not take into consideration the large number of observations (i.e., time points) within participants which substantially increases statistical power, especially when within participant variance in the dependent variable is high. Similar effect sizes are detectable in standard event-related and blocked design fMRI experiments but require many trials ( $k > 60$ ) or a larger sample ( $N > 30$ ) (Baker et al., 2021), both of which are far exceeded with the NNDb dataset.

## 2.4 Analysis plan

In order to investigate neural processing of social and semantic events and concepts, two primary types of scores were extracted from each movie: (1) event-level scores and (2) word-level scores. The movie event-level scores were generated via a manual coding process in which each movie was segmented into discrete events and the relative semantic and social content within events were rated independently. Movie word-level scores were generated by conducting a principal component analysis on 12 critical word property values and smoothing the resulting

scores using a sliding window. Both the word-level and event-level scores were used in parametric modulation analyses to assess the neural response to varied levels of lexical and event-based semantic and social content (RQ1) and the extent to which processing lexical and event-based semantic and social information relies on overlapping regions within the semantic and social brain networks within subjects (RQ2). The sections below provide additional detail on how these data were generated and the pre-registered analyses. See **Figure 2** for a schematic overview of the analyses.



**Figure 2. Schematic of planned analyses.** Representative events from one of the movies (*Back to the Future*) are shown in red, blue, and yellow shaded tiles. The corresponding event number, social and semantic rating, and event description are provided below the event screenshot. These events are sampled from the Event-Level time course (below the tiles) which shows the semantic (green) and social (blue) event ratings for the movie. Event 161 (blue tile) is used to illustrate how the words within events are processed. First, word properties are generated for all

transcript words. Second, missing data are imputed 5 times (ignoring closed class words which are shaded grey). Third, PCA is run on each of the imputed datasets, and the resulting factor scores from the 5 datasets are averaged. Only the averaged Semantic Flexibility and Social Impact factor scores are shown because these are the data that will be used for analyses. Fourth, the factor scores and semantic content (i.e., number of content words) are smoothed within the event boundaries. The summed total factor score or the number of content words is calculated within a 5s sliding window sliding every second. This window stops at the end of the event, and a new sliding window starts at the beginning of each event. When no words fall within a window (demonstrated with Event 282), the calculated window value is 0. This process results in a Word-Level time course of smoothed scores which is shown to the right of the Event-Level time course. Both the Event-Level and Word-Level time courses were used as parametric modulators by convolving the time courses with whole-brain BOLD signal (bottom panel). The semantic network and simulated BOLD time series are shown as an example.

#### 2.4.1 Movie events

To provide data at the event level, each movie was segmented into discrete events capturing subtle changes in the content or purpose of consecutive scenes. A detailed protocol was developed to provide consistent principles for segmenting. Manual subjective ratings of event boundaries have been previously applied to naturalistic movie data and have a high degree of correspondence with data-driven event segmentation models based on shifts in patterns of brain activity (Baldassano et al., 2017). For this study, event transitions were identified by the first author using the following criteria: (1) event boundaries are defined by a qualitative shift in the tone, setting, characters, or purpose of the scene; (2) a single event is often shot continuously with the same characters in the same setting or environment. Any sudden shift in the tone or emotional impact should be an indicator that a new event has begun; (3) the action sequences that occur within an event are more predictable than action sequences that occur between events. The latter criterion was derived from previous research on event prediction, which suggests that a good indicator of whether a new event has begun is if a sequence feels disconnected, unexpected, unrelated, or discontinuous from the previous sequence (Buchsbaum et al., 2015;

Zacks et al., 2011). Changes in background music or camera angles alone were not sufficient for marking an event boundary. Further, a distinction was made between *major events*, which tend to occur less frequently, have a longer duration (i.e., several minutes), and be accompanied by a larger shift in the content or purpose of a scene, and *minor events*, which occur more frequently, have a shorter duration (i.e., several seconds), and are signalled by more subtle shifts in content or purpose. Excluding opening studio credits and closing credits, the number of events per movie ranged from 238 to 429 ( $Mdn = 384$ ).

The semantic and social content of each minor event was rated for each movie. Both semantic and social content were rated on a scale from 1 to 10 with higher scores indicating greater semantic or social content. Semantic content was defined as narrative exposition in which movie or scene information is presented linguistically through spoken language (by a character or narrator) or in writing (such as text about the movie, timescale, or characters or any text presented during an event). Although semantic information can be expressed non-linguistically, this type of semantic knowledge requires a greater degree of inference which can be variable when manually coding events. To avoid conflating linguistic semantic information with non-linguistic semantic or pragmatic inferences, only spoken or written information was considered semantic content. For the purposes of this study, events in which new semantic information was presented were coded as more semantic relative to events with semantic content that was already known to the viewer. Critically, a distinction was made between novel information and shocking or surprising information, the latter of which did not receive a higher semantic score. Information was considered new only if it is being presented to the viewer for the first time. Events in which a character learns information the audience already knows would receive a lower semantic score. Such a scene may receive a higher social rating (described below) if the information is personally impactful or requires updating a false belief. This criterion was included because events with novel information are more informative and require greater semantic processing relative to the moments in which the information is consistent or has already been processed (because it has already been presented to the viewer). Low semantic events would have minimal to no written or spoken exchange of new information, such as an

action sequence. See [\*\*Appendix D: Supplementary Figure 1\*\*](#) for the detailed rubric for coding semantic information.

Social content was defined by the presence of more than one person or character, even if inanimate or off-screen. Any event that conveys information about the characters in the movie and their relationships with other characters was considered social. This could include general conversation or exchange of neutral character information, which would receive a low to moderate social rating, or could convey character attitudes, thoughts, feelings, or passions, which would receive a moderate to high social rating. The relative degree of sociality may depend on the type, duration, and significance of the interaction within the event. Events were considered more social if (1) the interpersonal connection between or among the characters was deeper and intense rather than superficial or brief based on their prior interactions throughout the movie and (2) the specific characters in the event bring a larger significance to the interaction based on who they are or the pre-defined relationship between or among the characters. A distinction was made between high social and high emotional content. Although an event may be both highly social and emotional, an event does not have to be emotionally intense in order to be considered social. Similarly, social and semantic content were coded independently as an event can be both highly (or weakly) social and semantic. The highest ratings (i.e., 9 or 10) were reserved for events in which the primary purpose of the scene was to convey semantic or social information. Importantly, a single event could not receive a 9 or 10 for *both* semantic and social content because the primary purpose had to be coded as either semantic or social. See [\*\*Appendix D: Supplementary Figure 2\*\*](#) for the detailed rubric for coding social information.

The first author watched all of the movies and marked the minor event boundaries using the established protocol. This was done to provide the event boundaries for coding semantic and social content and to ensure that the events of primary interest were coded in a consistent way across all 10 movies. At least 1 other independent coder then marked where the major events occurred within each movie using the established timestamps from the minor events.

After events were delineated, at least two independent coders (the first author and at least one independent coder) rated the semantic and social content of each minor event in the movie and wrote a brief description of what occurred during the

event (see **Table 1** for examples). Inter-rater reliability was assessed separately for the semantic and social scores for the coders of each movie using Krippendorff's alpha reliability coefficient. When the inter-rater reliability fell below .75, the coder who rated all movies identified which events were poorly aligned, rewatched the event, and made a revised consensus rating based on the content of the event and the notes of the other coder.

**Table 1***Example movie event annotations and smoothed word data*

Event Data			
Event Number	Semantic Score	Social Score	Event Notes
	R1 (R2)		
278	2 (3)	1 (1)	Doc waiting for Marty at the clock tower
279	5 (6)	6 (6)	Marty arrives and Doc rushes over
280	6 (6)	6 (6)	Marty explains how things went down with his dad. Doc seems worried
281	9 (9)	4 (6)	Doc explains plan to Marty
282	4 (5)	9 (10)	Marty and Doc say goodbye
283	7 (7)	6 (4)	Doc restates part of the plan + Marty gets in the car
284	7 (9)	5 (3)	Doc discovers letter in his coat + rips it up
285	3 (4)	4 (5)	Tree crashes down. Doc and Marty split up to fix cables
286	1 (3)	3 (5)	Doc runs up clock tower to throw cable over
287	7 (7)	6 (7)	Marty tries to tell Doc about the future again

Word Data				
	Word Length	Semantic Flexibility	Emotional Strength*	Social Impact
Positive	[Event 170]: ... <i>felt sorry for him cause her dad hit him with the car he hit me with...</i>	[Event 191]: ... <i>know what to say say anything say whatever's natural the first thing that comes into your mind...</i>	[Event 23]: ... <i>Dr Brown is dangerous he's a real nutcase hang around with him you'll end up in big trouble...</i>	[Event 221]: ... <i>I wish I wasn't so scared there's nothing to be scared of all it takes is self-confidence...</i>
Negative	[Event 281]: ... <i>I've calculated the precise distance taking into account the acceleration...</i>	[Event 151]: ... <i>the sink that's when you got the idea for the flux capacitor which...</i>	[Event 81]: ... <i>this tells you where you're going this where you are and this where...</i>	[Event 38]: ... <i>replace that clock thirty years ago lightning struck that clock tower and the clock...</i>

Note. Event Data: representative movie event annotations are taken from *Back to the Future*. Event 282 is used as an example in **Figure 2**. For the Semantic Score and Social Score ratings, the primary coder ratings (R1) are shown as well as ratings from a secondary coder (R2) which are shown in parentheses. Event Notes are from the primary coder (R1). Event Number refers to the Minor Event Number. Word Data: smoothed windows with high positive or negative summed total factor scores from *Back to the Future*. The event number from which each smoothed window is taken is indicated in brackets. \*using absolute value transformed scores.

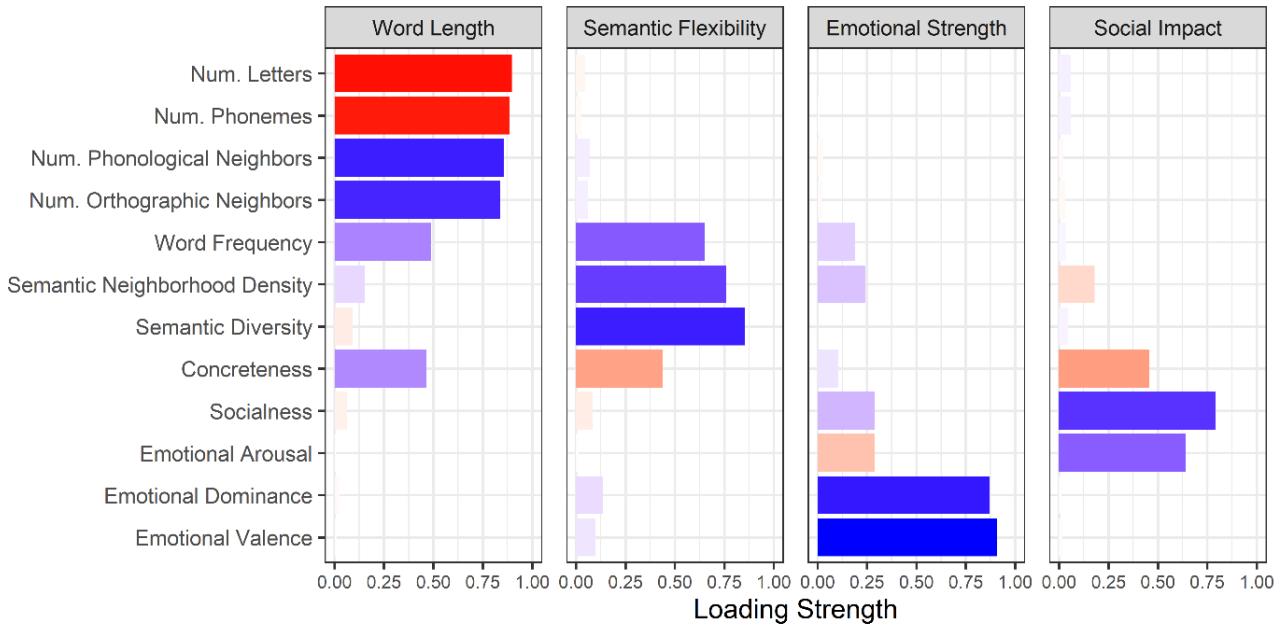
## 2.4.2 Movie transcripts

To provide data at the word level, the transcript annotations made available with the public dataset were used and included the words that were spoken as well as their onset and duration times. The initial paper describing the NNDb provides greater detail on the methods used for generating this information (Aliko et al., 2020). The following word properties were obtained, where available, for each word in the transcript annotations using the English Lexicon Project database (Balota et al., 2007): number of letters, number of phonemes, number of phonological neighbours, number of orthographic neighbours, word frequency, concreteness (Brysbaert & New, 2009), semantic neighbourhood density, semantic diversity (Hoffman et al., 2013), emotional valence (i.e., pleasantness), emotional arousal (i.e., intensity), and emotional dominance (i.e., control) (Warriner et al., 2013), and part of speech.

To obtain ratings of socialness for each word spoken in the movies, social word ratings were generated from a previous norming study conducted with 68 participants from the University of Alabama at Birmingham. Candidate words were derived from the Glasgow norms study, which includes normative psycholinguistic ratings for over 5,000 individual words (Scott et al., 2018). This initial list was filtered to remove words with high concreteness ( $> 5$ ) and imageability ( $> 5$ ) ratings in order to identify possible social concepts (which tend to be abstract, although see (Diveica et al., 2023)) as norming targets. Additional target words were added from a study reporting social desirability ratings on over 500 words (Hampson et al., 1987). A randomly selected subset of 688 words were included in the norming study, and words with varied parts of speech were intentionally retained. During the norming study, participants were instructed that a word is social if it describes inter-personal behaviours, motivations, intentions, or characteristics and were asked to rate how social each presented word was on a scale from 1 (not social) to 5 (very social). Each participant rated half of the words resulting in 34 ratings for each of the 688 unique words. For words not present in this set of 688 words, social ratings were extrapolated by calculating their semantic similarity to each of the words in the normed set. Semantic vectors were generated for each of the normed words as well as for the unique transcript words using word2vec. The cosine similarity between each transcript word and every normed word was calculated resulting in 688 similarity values for each transcript word. The average social rating was then

calculated by taking a weighted average, using the cosine similarity, of the social scores from the 10 closest semantic neighbours.

Prior to subsequent analyses, the unique words from all movies were combined; high frequency and closed class words were excluded, as were any words missing more than 10 of the 12 critical word properties (excluding part of speech). To avoid listwise deletion, missing data for the remaining set of words were imputed. Imputation was performed using the multiple imputation by chained equations approach implemented with the *mice* package in R (van Buuren & Groothuis-Oudshoorn, 2011), and resulted in 5 complete datasets. To reduce covariance between predictors, the 12 word property measures for each unique word were entered into a principal component analysis (PCA) with varimax rotation for each imputed dataset. The four factor result corresponded to Word Length (e.g., number of letters and phonemes, number of phonological and orthographic neighbours), Semantic Flexibility (e.g., semantic diversity, semantic neighbourhood density), Emotional Strength (e.g., emotional valence, emotional dominance), and Social Impact (e.g., socialness, emotional arousal) and accounted for approximately 29%, 17%, 16%, and 11% of the variance respectively (**Figure 3**). The Emotional Strength factor scores were transformed by taking the absolute value in order to capture emotional versus neutral content rather than positively versus negatively valenced content. The resulting factors were stable across the imputed datasets and resulted in the same factors as a PCA run on a subset of the data with no missing values. Due to random variation introduced when imputing data and given the robustness of the results, the factor scores derived from the imputed datasets were averaged.



**Figure 3. Factors derived from PCA on word property values.** Positive (blue) and negative (red) loadings are shown for each factor. The strength of the loading is indicated by the length and colour saturation of each bar. Num., Number.

#### 2.4.3 Aligning annotations and events

The transcript annotations were temporally aligned with the events using the event boundary timestamps and the onset times of each word. Different versions of the movie files may have slightly varying playback speeds (+/- 1.5%). To ensure correct alignment, the events were marked and aligned using the same movie files that were presented to participants in the NNDb study. This was done to identify which words were present within each event. To account for hemodynamic lag, a smoothed time course of critical word-level factor scores was generated by summing values within a 5s window sliding every 1s. A data-driven event segmentation approach with comparable movie data found that the median duration of neural states across voxels ranged from 5 to 18.5s, and these durations were reliable across participants (Geerligs et al., 2022). A 5s window is thus advantageous as it would capture the regions with shorter neural state durations (predominately sensory processing areas) and provide multiple measurements of the neural state of those regions with longer durations (e.g., default mode network). Importantly, the sliding windows were constrained to each event's boundaries so word property scores from different events were not averaged together (see **Table 1** for examples). Events with

excessively short duration (< 3s; 4% of events) were merged with the subsequent event by taking the average semantic and social score across the two events. After merging short events, the event duration ranged from 4 to 131s ( $Mdn = 16.00$ s). If an event was shorter than the window size of 5s, the sum was calculated within this smaller window. If the final portion of an event was less than 1 second (i.e., 500ms), a slightly shorter window was defined, and the sum was calculated within the smaller window. For each factor, the residuals were extracted from a model predicting the smoothed factor time course from the number of total words within each window. This will control for the number of words in an event. If there are no words or no words that have ratings within a window or event, a value of 0 will be assigned for each factor score.

General lexical-semantic content was quantified by counting the number of content words (i.e., open class words). Open class words with missing word property data ( $n=883$ ) which were excluded from the PCA (and subsequently do not have factor scores) were still counted as semantic content by manually tagging part of speech. These include character names, dates, or movie-specific words (i.e., fictional towns, technology, slang) that were not found in psycholinguistic databases. The same sliding window approach was used to generate a smoothed time course of lexical-semantic content. This predictor, as well as the factor scores, captures the momentary quantity of basic conceptual knowledge within each window, agnostic to the preceding events, which likely under approximates the amount of semantic processing occurring and is not sensitive to detecting pragmatic inference or non-linguistic semantic processing. This approach was adopted here because it most closely aligns with how prior studies examined semantic processing of isolated words or sentences, and one of the goals of the current study was to examine these measures in a naturalistic context. The event-level semantic predictor similarly indexes only the linguistic information in events, but is informed by prior context and may better capture broader context-sensitive semantic processing.

#### 2.4.4 Network definitions

The networks of interest were defined using statistical maps derived from independent coordinate-based activation likelihood estimation (ALE) analyses of semantic control, semantic cognition, and social cognition and are shown in **Figure**

1. These network maps were used to aid in the interpretation of the results of the whole brain analyses by categorizing results as falling within or outside of the pre-defined networks. The semantic and social networks in particular are extensive, and it is likely to be minimally informative to look at percent overlap or Dice similarity coefficient in isolation. For this reason, greater emphasis was placed on *where* overlap between the resulting networks and the pre-defined networks occurs. Overlap in core regions within each ALE-generated network, highlighted in the top portion of **Figure 1**, was interpreted as stronger evidence of network involvement. Defining networks prior to analysis ensured that results were interpreted in a pre-specified manner.

The semantic control network was defined based on an ALE analyses with over 120 contrasts from 87 studies which identified a large cluster centred around the left inferior frontal gyrus as well as posterior middle temporal gyrus, dorsomedial prefrontal cortex, and a smaller portion of the right inferior frontal gyrus (Jackson, 2021). This network has significant convergence with another ALE-generated semantic control network (Diveica et al., 2021). The same study also identified a general semantic cognition network derived from over 400 contrasts from 257 studies. In order to isolate the automatic semantic network and partial out the role of control in semantic retrieval, the semantic control ALE result was subtracted from the general semantic cognition ALE result and small clusters of voxels (< 400 contiguous voxels) were removed. This resulted in a map which included left anterior temporal lobe, left medial and posterior temporal cortex, left inferior parietal lobule, insula, precentral gyrus, and right middle and superior temporal gyrus.

The social cognition network was defined by examining the convergence of ALE generated network maps for four primary domains of social cognition from a previous study (Diveica et al., 2021). These domains included theory of mind (derived from 136 experiments), trait inference (derived from 40 experiments), empathy for pain or affective states (derived from 163 experiments), and moral reasoning (derived from 68 experiments). The ALE results for each domain were overlaid and regions which were identified in at least one of the four domains were retained. This resulted in a social network which included bilateral inferior frontal gyrus, superior frontal gyrus, medial prefrontal cortex, precuneus, bilateral inferior parietal lobule, supplementary

motor area, bilateral anterior and superior middle temporal gyrus, bilateral anterior temporal poles, and precentral gyrus.

## 2.5 Statistical analyses

The pre-processed MRI data were used for all analyses. The pre-processing steps are documented in the initial paper describing the NNDb dataset (Aliko et al., 2020). The functional runs were concatenated into a single timeseries file after detrending and censoring TRs with excessive motion. There are no missing data for the current set of 86 participants that comprise the NNDb. The only data that are missing are word property values, but the approach to dealing with those data are outlined in detail above. The NNDb data includes quality assurance metrics indexing movement related artefacts and signal to noise. Given that the metrics indicate that the data are high quality (mean temporal signal to noise ratio [tSNR] > 60) and the scan duration was sufficiently long for detecting activation at that tSNR level (> 1 hour) (Murphy et al., 2007), none of the participants were excluded from analysis.

### 2.5.1 Research question 1

For the word-level analyses, the Semantic Flexibility factor was used in the semantic control analysis because semantic diversity (Hoffman et al., 2013) and semantic neighbourhood density (Diaz et al., 2022; Mirman & Graziano, 2013) reflect increased selection demands which requires additional cognitive control. The Social Impact factor was used as a proxy of social content, and the number of content words was used as a coarse measure of semantic content. These measures were each separately used as parametric modulators in a regression model predicting the time series from the full movie. The analyses were conducted at the whole-brain level, and results were compared to the predefined networks of interest. The subject-level activation maps for each content type for all movies were used as inputs for a second-level group analysis using linear mixed-effects modelling with a fixed effect of content type (i.e., social, semantic, or semantically flexible) and random intercepts of subject and movie implemented using 3dLMEr in AFNI (Chen et al., 2013). The resulting statistical map were corrected using a cluster-forming threshold of  $p < 0.01$  and an FWE-corrected threshold of  $p < 0.05$ .

For the event-level analyses, the semantic and social event ratings for each movie were used in a first-level general linear model for each subject as parametric modulators predicting the time series from the full movie. To account for the varied event durations, a duration modulated model was used in which the onset and duration of each event were included in the regression model. Either semantic or social content were included as a nuisance regressor. In addition, the ratings were randomly scrambled to generate a null distribution which served as a comparison condition with no semantic or social content. The analyses were conducted at the whole-brain level. The subject-level activation maps across all movies were used as inputs for a second-level group analysis using linear mixed-effects modelling with a fixed effect of content type (i.e., social or semantic or null) and random intercepts of subject and movie implemented using 3dLMEr in AFNI (Chen et al., 2013). The resulting statistical map was corrected using corrected using a cluster-forming threshold of  $p < 0.01$  and an FWE-corrected threshold of  $p < 0.05$ .

## 2.5.2 Research question 2

To investigate the extent to which the social system shares neural resources with the semantic and semantic control systems within individual subjects, the subject-level statistical maps generated to test research question 1 were directly compared. Specifically, the number of overlapping voxels was calculated between (1) the statistical maps for processing semantic and social content (word-level and event-level results processed independently) and (2) the statistical maps for processing semantically flexible words and social words. The presence of voxels that respond to *both* semantic and social concepts or events was taken as evidence of shared neural resources between the systems. The strength of the evidence was determined by the number of overlapping voxels quantified using Dice coefficient, and fewer than 10 overlapping voxels was considered functionally the same as 0 voxels. Overlap within the semantic hub in ATL will provide support for the *graded semantic hub hypothesis* which suggests that both systems rely on the same domain-general hub. Non-overlapping, proximal clusters of voxels that differentially respond to semantic (or semantic control) and social content in the absence of any overlapping voxels will provide weaker evidence of shared processing between the systems, and instead will be interpreted as evidence for graded functioning within a semantic or social

network region. To determine the extent to which stable areas of overlap between the cognitive systems exist across participants, a second-level random effects analysis was run using the overlap images from individual participants. The group-level overlap maps were compared to the predefined ALE-derived network definitions to determine the extent to which the core regions within each network (shown in **Figure 1**) were involved in each process and to isolate any regions which fall outside the expected networks.

### 3 Results

#### 3.1 Research question 1

The Words and Events results are shown in the following sections with two cluster correction thresholds applied: (1) the pre-registered threshold (cluster-forming threshold of  $p < 0.01$  with an FWE-corrected threshold of  $p < 0.05$ ) and (2) a more conservative threshold (cluster-forming threshold of  $p < 0.01$  with an FWE-corrected threshold of  $p < 0.01$ ). The latter threshold was applied in an effort to highlight areas with the strongest response to the stimulus alongside the values that fall below that threshold (Taylor et al., 2023). The results figures indicate which voxels survived each cluster threshold and tables report clusters that survived the pre-registered threshold. Results figures were generated using MRIcroGL (Rorden & Brett, 2000).

##### 3.1.1 Words analysis

The word-level predictor variables were generated as described in the pre-registered Methods section with one minor deviation. The pre-registration indicated that when a window or event contained no words or no words that had ratings, a value of 0 would be assigned for each factor score. However, because scores were mean-centred, a score of 0 corresponds to words with an average factor score, not the absence of a score as initially intended. In addition, given the visual nature of movie stimuli, as opposed to narratives, there are many events that do not contain words. As a result, many windows containing few, if any, words would have been modelled as containing words with average factor scores. This was not justifiable on scientific grounds, so windows with no words or no words with ratings were removed from analysis instead. This error was realized and corrected prior to running the

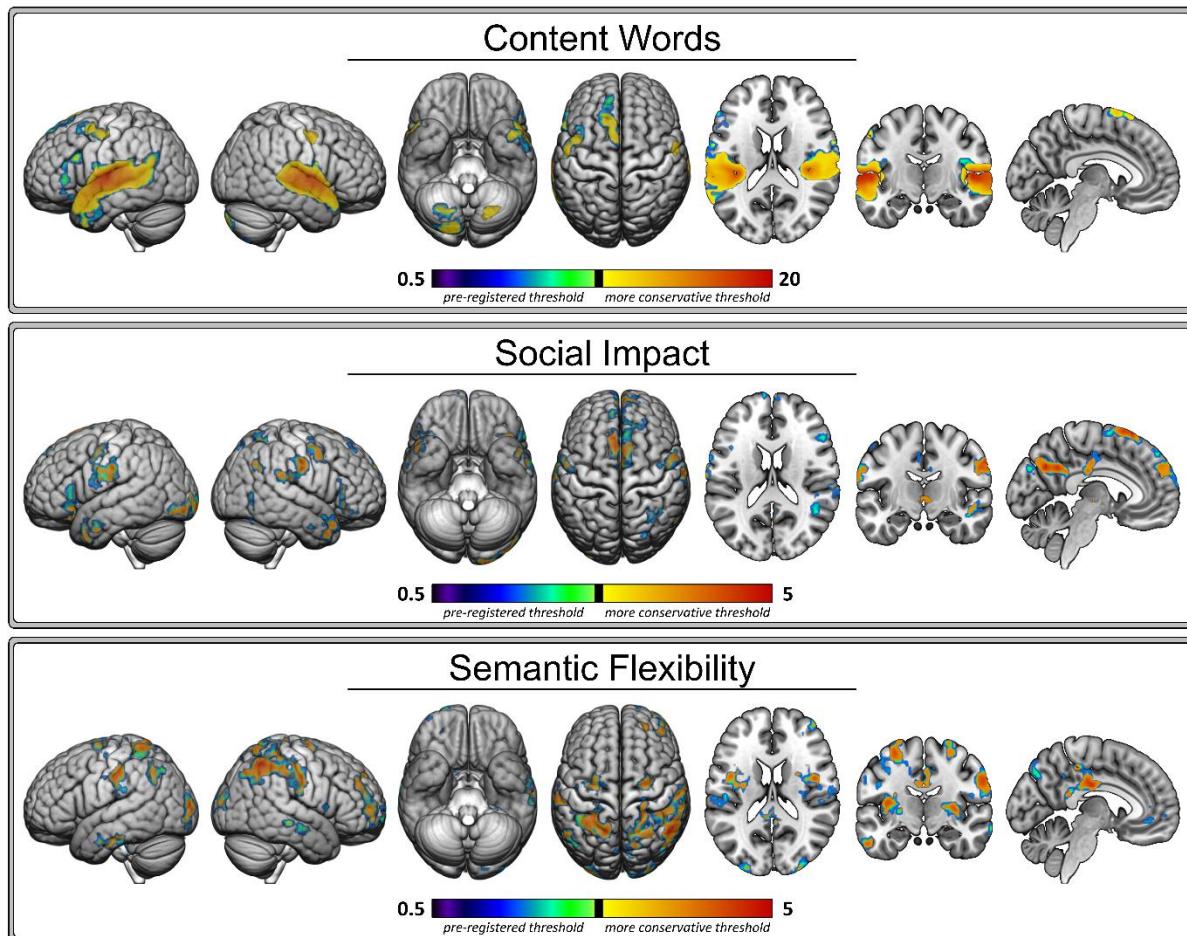
words analyses. The words analysis results are shown in **Figure 4** and the coordinate information is provided in **Table 3**.

**Number of Content Words.** It was expected that clusters of voxels showing increased activation in response to greater semantic word-level content (i.e., number of content words) would fall within the semantic brain network (Hypothesis 1.1a). In line with this prediction, an increase in the number of content words was positively associated with activation in broad bilateral clusters extending from anterior to posterior superior temporal gyri with peak voxels in auditory cortices. The left hemisphere cluster was more extensive, including the superior and lateral portions of the temporal pole (the lateral portion is sometimes labelled “ventrolateral ATL” (Binney et al., 2010; Lambon Ralph et al., 2017), though the present results did not extend to the ventral portion of ATL), middle temporal, supramarginal, and angular gyri. Frontal activation was observed in smaller clusters in left inferior frontal, middle frontal, and superior frontal gyri and supplementary motor area and left precentral gyri. Cerebellar activation, predominately in the right posterior lobe of the cerebellum, also positively co-varied with the number of content words.

**Social Impact.** It was expected that clusters of voxels showing increased activation in response to greater social word-level content (i.e., Social Impact scores) would fall within the social brain network (Hypothesis 1.1b). In line with this prediction, an increase in social and emotionally arousing words (indicated by positive Social Impact scores) was associated with activation in precuneus, right inferior parietal lobule (i.e., temporo-parietal junction [TPJ]), and frontal activation in bilateral inferior frontal gyri, superior medial gyrus, supplementary motor area, right precentral and middle frontal gyri, and left postcentral gyri. Activation in bilateral anterior middle (i.e., ventrolateral ATL) and superior (i.e., dorsolateral ATL) portions of the temporal pole also positively co-varied with Social Impact, as did clusters in right inferior temporal gyrus and fusiform and left inferior occipital gyrus.

**Semantic Flexibility.** It was expected that clusters of voxels showing increased activation in response to semantically flexible word-level content would fall within the semantic control brain network (Hypothesis 1.1c). Counter to this prediction, activation in left IFG and pMTG did not positively co-vary with Semantic Flexibility. Instead an increase in more frequent, semantically diverse words (indicated by positive Semantic Flexibility scores) was associated with activation in a large cluster

with a peak voxel in right postcentral gyrus that included portions of middle cingulate cortex, inferior and superior parietal lobule, and precuneus. Activation in a smaller, analogous left hemisphere region positively co-varied with Semantic Flexibility as did clusters in anterior cingulate, right middle and superior frontal gyri, left precentral gyrus, bilateral insula, left inferior temporal and fusiform gyri, left angular gyrus, and bilateral middle occipital gyrus.



**Figure 4. Words analyses results.** Thresholded Z-score statistical maps showing the number of content words (top panel), Social Impact (middle panel), and Semantic Flexibility (bottom panel) results. All clusters survived the pre-registered cluster threshold. The clusters that survived an additional, more conservative threshold are indicated in yellow (lower) to red (higher). The clusters that did not survive the more conservative threshold are shown in purple (lower) to green (higher).

**Table 2***Words results coordinate table*

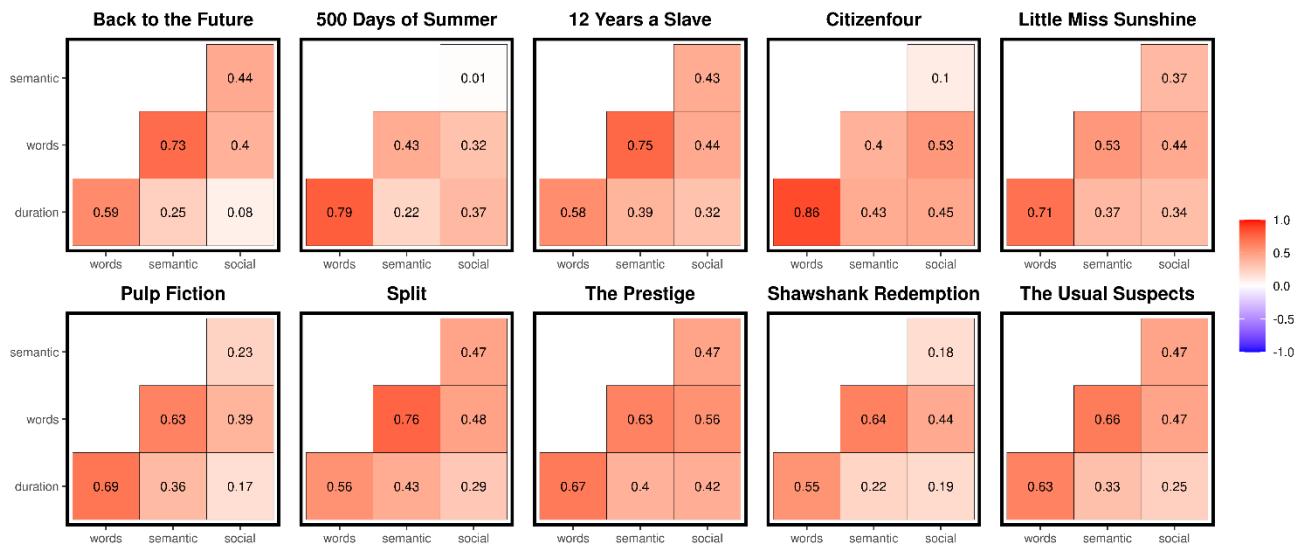
Variable	Cluster Size	Hem	Brain Region Peak Voxel	Brain Region Highest Overlap [%]	MNI Coordinates		
					X	Y	Z
<i>Content Words</i>	2558	L	Superior Temporal Gyrus	Middle Temporal Gyrus [30%]	-53	-20	7
	1689	R	Heschl's Gyrus	Superior Temporal Gyrus [42%]	50	-14	7
	418	R	Cerebellum (VII)	Cerebellum (Crus 2) [32%]	17	-83	-57
	175	L	Supplementary Motor Area	Superior Frontal Gyrus [41%]	-5	4	77
	149	L	Postcentral Gyrus	Precentral Gyrus [29%]	-56	-10	57
	117	L	Inferior Frontal Gyrus (Triangularis)	Inferior Frontal Gyrus (Triangularis) [76%]	-56	16	29
<i>Semantic Flexibility</i>	2423	R	Inferior Parietal Lobule	Postcentral Gyrus [17%]	53	-57	51
	802	L	Superior Parietal Lobule	Postcentral Gyrus [27%]	-17	-64	73
	471	R	Putamen	Putamen [32%]	32	4	5
	375	R	Middle Frontal Gyrus	Middle Frontal Gyrus [58%]	41	51	8
	331	L	Insula Lobe	Insula Lobe [35%]	-32	1	5
	284	R	Middle Orbital Gyrus	Middle Orbital Gyrus [19%]	8	39	-7
	259	L	Cerebellum (VI)	Fusiform Gyrus [39%]	-26	-43	-33
	220	L	Inferior Occipital Gyrus	Middle Occipital Gyrus [84%]	-26	-91	-3
	169	L	Precentral Gyrus	Precentral Gyrus [55%]	-29	-17	66
	168	R	Middle Occipital Gyrus	Middle Occipital Gyrus [53%]	29	-95	10
	116	R	Superior Frontal Gyrus	Superior Frontal Gyrus [83%]	26	-11	76
	110	L	Angular Gyrus	Angular Gyrus [35%]	-53	-66	44
	99	L	Inferior Temporal Gyrus	Inferior Temporal Gyrus [67%]	-56	-12	-38
	99	R	Middle Temporal Gyrus	Middle Temporal Gyrus [91%]	65	-29	-14
<i>Social Impact</i>	576	L	Precuneus	Precuneus [30%]	-5	-68	31
	463	L	Inferior Frontal Gyrus (Orbitalis)	Inferior Frontal Gyrus (Orbitalis) [24%]	-32	18	-19
	383	R	Inferior Frontal Gyrus (Orbitalis)	Inferior Frontal Gyrus (Orbitalis) [25%]	38	24	-18
	367	L	Postcentral Gyrus	Postcentral Gyrus [43%]	-71	-15	24
	341	L	Supplementary Motor Area	Supplementary Motor Area [44%]	-8	20	74
	335	R	Superior Medial Gyrus	Superior Medial Gyrus [43%]	5	62	31
	300	R	Postcentral Gyrus	Supramarginal Gyrus [40%]	62	-16	40
	252	R	Superior Temporal Gyrus	Superior Temporal Gyrus [43%]	44	-29	-7

222	L	Lingual Gyrus	Inferior Occipital Gyrus [32%]	-17	-103	-15
162	R	Superior Parietal Lobule	Superior Parietal Lobule [58%]	35	-57	57
159	R	Angular Gyrus	Angular Gyrus [64%]	50	-59	28
138	R	Cerebellum (Crus 1)	Inferior Temporal Gyrus [38%]	47	-62	-27
115	R	Middle Cingulate Cortex	Middle Cingulate Cortex [32%]	-2	-24	26
111	R	Precentral Gyrus	Precentral Gyrus [79%]	50	-7	57

Note. This table was generated based on the pre-registered cluster threshold. Cluster size is determined by the number of 2mm<sup>3</sup> voxels. MNI coordinates correspond to the voxel with peak activation within each cluster. Voxels were defined as neighbours based on faces touching (NN=1). Atlas labels are based on the Eickhoff-Zilles macro labels from the N27 (MNI space) atlas. Hem, Hemisphere; L, Left; R, Right.

### 3.1.2 Events analysis

Correlations between the event properties, including semantic and social ratings, are shown in **Figure 5**. Predictably, event duration and the number of words within an event were moderately to highly correlated ( $r = 0.55-0.86$ ). Semantic ratings were positively correlated with number of words ( $r = 0.40-0.76$ ), as were social ratings to a lesser extent ( $r = 0.32-0.56$ ). This is unsurprising given that highly semantic events were defined as having new or informative verbal content and, to some extent, social moments in movies often rely on, or are supplemented by, verbal input. Although positively correlated, it was not the case that event ratings were simply proxies for duration or word quantity. Further, the semantic and social ratings did not capture the same event properties, as evidenced by the low to moderate correlations between the ratings ( $r = 0.01-0.47$ ).



**Figure 5. Event property correlations.** Bivariate correlations between the number of words in an event, event duration, semantic rating, and social rating.

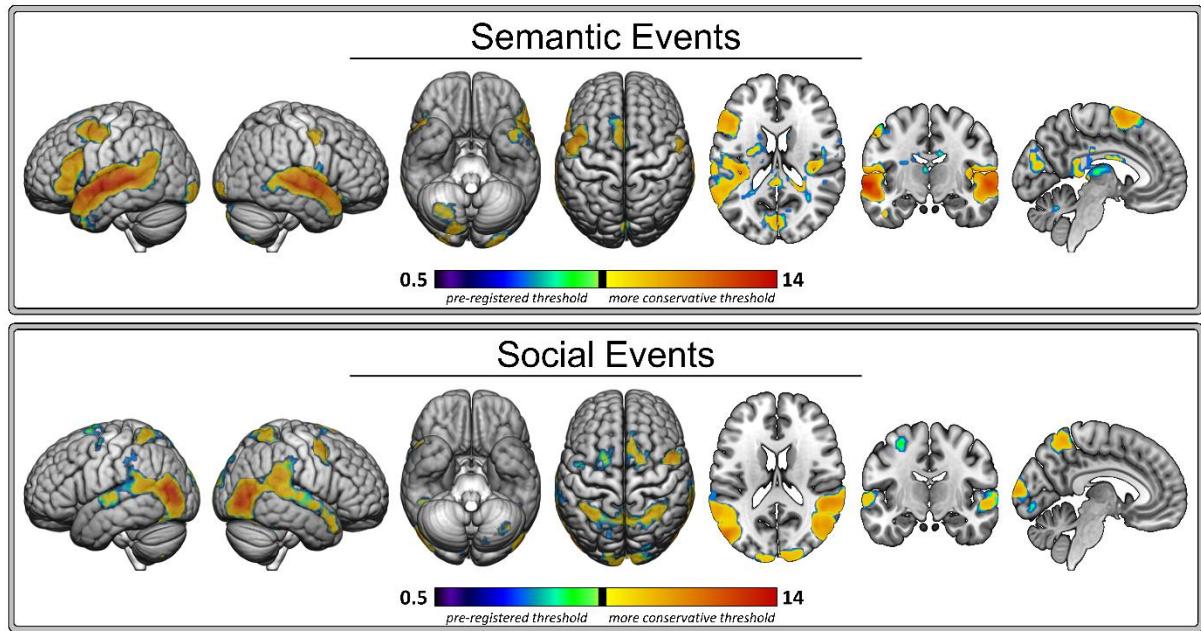
The events analysis results are shown in **Figure 6** and the coordinate information is provided in **Table 3**. The following sections provide an overview of the results for the pre-registered events analyses.

**Semantic Events.** It was expected that clusters of voxels showing increased activation in response to semantic events (plot-progressing, informative verbal or

written scenes) would fall within the semantic brain network (Hypothesis 1.2a). In line with this prediction and the number of content words results, there was increased activation in the canonical language network as the semantic content in events increased. Similar to the content words results, there were large bilateral clusters centred around auditory cortices and extending from posterior to anterior superior temporal gyrus. The left hemisphere cluster included the middle portion of the temporal pole (i.e., lateral ATL) and extended posteriorly into inferior parietal lobule. There was also a large left inferior frontal gyrus cluster and a cluster in left supplemental motor area. Additional clusters of activation were observed in left cuneus and calcarine gyrus and inferior occipital gyrus and the right posterior lobe of the cerebellum. Subcortical activation positively co-varied with semantic event content in left putamen, thalamus, caudate nucleus, and a portion of the hippocampus.

**Social Events.** It was expected that clusters of voxels showing increased activation in response to social events (scenes depicting on or off-screen interactions between/among characters) would fall within the social brain network (Hypothesis 1.2b). In line with this prediction, as the social content in events increased, there was increased activation in bilateral inferior parietal lobule (i.e., TPJ), left fusiform, precentral and middle frontal gyri, and supplementary motor area. Smaller clusters of activation in left calcarine and superior occipital gyri and a small cluster in the posterior lobe of the left cerebellum also positively co-varied with social event content. There were also prominent effects in bilateral lateral occipitotemporal cortex, which is typically associated with motion processing (V5/MT) and object recognition (LOC) rather than social cognition. Unlike the Social Impact words analysis results, social event content did not engage the left anterior temporal lobe.

**Scrambled Events.** Scrambled semantic and social ratings were used as a negative control condition for comparison with the critical predictions. There were no surviving clusters of activation positively associated with the scrambled ratings at either cluster correction threshold.



**Figure 6. Events analyses results.** Thresholded Z-score statistical maps showing the Semantic Events (top panel) and Social Events (bottom panel) results. All clusters survived the pre-registered cluster threshold. The clusters that survived an additional, more conservative threshold are indicated in yellow (lower) to red (higher). The clusters that did not survive the more conservative threshold are shown in purple (lower) to green (higher).

**Table 3***Events results coordinate table*

Variable	Cluster Size	Hem	Brain Region Peak Voxel	Brain Region Highest Overlap [%]	MNI Coordinates		
					X	Y	Z
Semantic Events	3690	L	Middle Temporal Gyrus	Middle Temporal Gyrus [25%]	-56	-33	-0
	1916	R	Superior Temporal Gyrus	Superior Temporal Gyrus [34%]	65	-1	-2
	807	R	Precuneus	Putamen [8%]	23	-46	16
	745	R	Cerebellum (Crus 2)	Cerebellum (VIII) [26%]	20	-86	-50
	354	L	Calcarine Gyrus	Cuneus [35%]	-2	-83	14
	232	L	Supplementary Motor Area	Supplementary Motor Area [87%]	-5	1	74
	172	L	Lingual Gyrus	Inferior Occipital Gyrus [31%]	-26	-100	-18
Social Events	2545	R	Inferior Occipital Gyrus	Superior Temporal Gyrus [25%]	50	-79	-6
	1576	L	Middle Occipital Gyrus	Middle Temporal Gyrus [31%]	-53	-79	7
	1035	R	Superior Parietal Lobule	Superior Parietal Lobule [21%]	35	-57	64
	601	L	Superior Occipital Gyrus	Calcarine Gyrus [19%]	-5	-101	6
	243	R	Middle Frontal Gyrus	Precentral Gyrus [65%]	50	2	54
	218	L	Cerebellum (VIIb)	Cerebellum (VII) [30%]	-14	-76	-60
	178	L	Superior Frontal Gyrus	Precentral Gyrus [53%]	-20	-2	77
	159	R	Supplementary Motor Area	Supplementary Motor Area [59%]	8	10	77

Note. This table was generated based on the pre-registered cluster threshold. Cluster size is determined by the number of 2mm<sup>3</sup> voxels. MNI coordinates correspond to the voxel with peak activation within each cluster. Voxels were defined as neighbours based on faces touching (NN=1). Atlas labels are based on the Eickhoff-Zilles macro labels from the N27 (MNI space) atlas. Hem, Hemisphere; L, Left; R, Right.

## 3.2 Research question 2

### 3.2.1 Subject-level cognitive system overlap

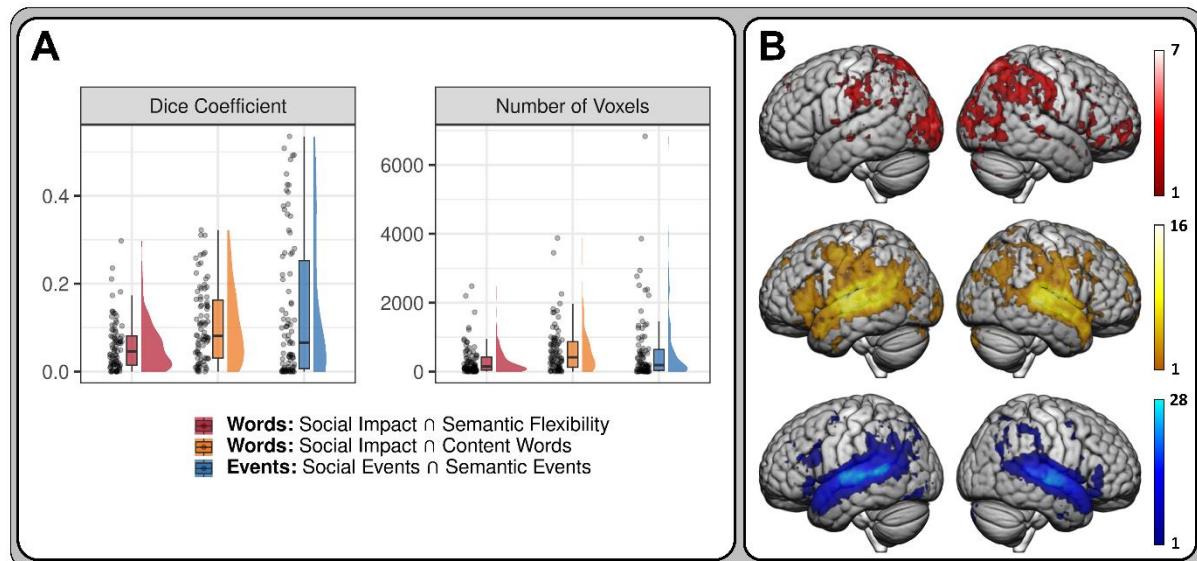
There was considerable variability in the cognitive system overlap at the subject-level. The Dice similarity coefficients and the number of overlapping voxels between the thresholded subject-level statistical maps are presented in **Figure 7A**. There was modest overlap for Social Impact  $\cap$  Semantic Flexibility: median Dice coefficient = 0.05 (range: 0-0.30), median overlapping voxels = 146 (range: 0-2481). Somewhat more overlap was observed for Social Impact  $\cap$  Content Words: median Dice coefficient = 0.08 (range: 0-0.32), median overlapping voxels = 417 (range: 0-3879). Overlap for Social Events  $\cap$  Semantic Events was particularly variable: median Dice coefficient = 0.07 (range: 0-0.54), median overlapping voxels = 191 (range: 0-6829). In each case, the distributions were strongly skewed such that many participants showed relatively little overlap and a small subset of participants showed moderate cognitive system overlap.

### 3.2.2 Cross-subject cognitive system overlap

The pre-registered group-level analysis was intended to determine the extent to which stable areas of overlap existed across participants, but it was not able to answer this research question. Instead of identifying consistent areas of overlap, the analysis produced an aggregate map of *any* overlap observed at the subject-level. This result is misleading as it would give the impression of much greater cross-subject overlap which would result in making the wrong inferences about the cognitive systems being investigated.

Overlap maps showing the number of participants with subject-level overlap of cognitive systems at each voxel are presented in **Figure 7B**. The maps have been thresholded to only include areas of subject-level overlap that were observed in at least 2 participants. As evident from the figure, the amount of cross-subject overlap was minimal, especially for the Social Impact  $\cap$  Semantic Flexibility (max overlap = 7 participants). Where cross-subject system overlap occurred, the most consistent location of overlap between the cognitive systems was in bilateral superior temporal gyri and auditory cortices, likely driven by the amount of verbal input (i.e., number of words) which was correlated with the event ratings and inherent to the factor scores.

This region included the point of highest overlap ( $\text{Social Events} \cap \text{Semantic Events}$ ), but it was only 28 of 86 participants (32.6% of the sample), which does not suggest strong consistency.



**Figure 7. Overlap analysis results.** The subject-level cognitive system overlap, measured with Dice Coefficient and Number of voxels, is shown for the Social Impact  $\cap$  Semantic Flexibility (red), Social Impact  $\cap$  Content Words (orange) and Social Events  $\cap$  Semantic Events (blue) results in panel A. The cross-subject cognitive system overlap is shown in panel B. The overlap maps correspond to the Social Impact  $\cap$  Semantic Flexibility (red), Social Impact  $\cap$  Content Words (orange) and Social Events  $\cap$  Semantic Events (blue) cross-subject overlap. Each voxel represents the number of participants that had overlap at that voxel. All maps were thresholded to include only those areas where the subject-level overlap was at least 2.

## 4 Discussion

### 4.1 Overview

The present study investigated the neural basis of semantic and social processing during movie-viewing, which provides a rich estimation of the multimodal environment in which language use and social interactions take place (Jääskeläinen et al., 2021). Current neurobiological models of the semantic and social cognition systems were derived from experimentally controlled stimuli presented in random order without larger-scale context. Naturalistic stimuli are less constrained and tend to elicit activation in areas that show minimal response in minimalist experiments and to evoke highly stable patterns of brain activation, allowing for different insights into fundamental aspects of human cognition (Hasson et al., 2010). In order to comprehensively capture semantic and social content within the movies, word and event-level predictors were generated and used for analyses. The goals of the study were twofold. The first aim was to test the degree to which semantic and social content was processed within each network. The second, complementary aim was to test the degree to which the semantic and social systems evidence shared processing in the same regions or domain-general hub, given the conceptual and neural overlap between these systems.

In line with our predictions, word and event-level semantic content isolated a highly convergent, largely fronto-temporo-parietal network, despite measuring semantic content in different ways. Frequent, semantically diverse language (estimated by positive Semantic Flexibility scores) did not co-vary with activation in semantic control regions, counter to our expectations. An increase in both word and event-level social content engaged portions of the social, semantic, and semantic control networks, providing partial support for our hypotheses. Further, there were no positive associations with the scrambled ratings, increasing confidence that we report meaningful associations with the semantic and social event ratings. We did not observe stable, cross-subject overlap between semantic and social processing. All analyses and interpretations given to results were pre-registered prior to conducting the study. The following sections provide an overview of each content type, indicating, where relevant, when an interpretation that was not pre-registered is provided.

## 4.2 Semantic content

Activation in semantic and semantic control network regions positively co-varied with an increase in both word and event-level semantic content in complex movie stimuli. This network included the core regions highlighted in the meta-analytic map shown in **Figure 1**: bilateral ATL, bilateral middle temporal gyrus, left supplementary motor area, left IPL, semantic control regions in left inferior frontal gyrus and posterior middle temporal gyrus, and minimally included activation outside these networks. We made no specific predictions about the recruitment of the semantic control system in response to content words or highly semantic events because we had no corresponding measure of how cognitively demanding the words or events were (with the exception of Semantic Flexibility, discussed below). However, engagement of the semantic control system is routinely found in studies of semantic cognition and – unless they are explicitly removed – these control regions are found in meta-analyses of semantic cognition (Binder et al., 2009; Jackson, 2021). For the present study, semantic control regions were subtracted from the semantic system in order to distinguish automatic semantic processing regions from those regions which are involved in more effortful or controlled semantic processing. This suggests that control processes are an integral part of how the semantic system operates in naturalistic comprehension.

The fronto-temporo-parietal network observed here has considerable overlap with the ‘universal language network’ that has been identified across diverse languages (Malik-Moraleda et al., 2022). Convergence with the topography of this network is notable because it was derived with a different naturalistic paradigm - stories - using a contrast with acoustically degraded audio (or unfamiliar language) to identify the network of regions sensitive to language. The present study used continuous measures of high versus low semantic content to isolate regions that are particularly sensitive to an increase in semantic content. This focus on semantic content may explain why we observed more activation in the lateral portion of the ventrolateral ATL, which was only present in some of the language networks (including English) reported by Malik-Moraleda et al.

Correspondence with the universal language network suggests that there is a robust language comprehension network that is engaged across naturalistic contexts, including narratives and movies. Indeed, this network is well positioned to

serve this purpose with structural connections between orbitofrontal cortex and temporal pole (uncinate fasciculus), inferior frontal cortex to posterior superior temporal cortex (arcuate fasciculus) and inferior parietal lobule (extreme capsule) (Shekari & Nozari, 2023). Although not part of the semantic or language network, activation in right posterior cerebellar lobe may be similarly driven by the structural connections projecting into perisylvian language areas, suggesting a possible role in general language processing (Vias & Dick, 2017). A similar network topography has been reported in other studies that used naturalistic stimuli, predominately narratives and natural language (Wu et al., 2022; Zhang et al., 2020). Individual studies using minimalist stimuli tend to report highly focal results, however, aggregation of study-level data via meta-analysis reveals a network with similar topography to that observed here (Binder et al., 2009; Jackson, 2021), although naturalistic stimuli tend to evoke a more bilateral network.

The semantic content in complex movie stimuli was quantified using a word-level and an event-level definition, and, although both measures were used as proxies of semantic processing, it is nonetheless striking that they isolated a highly convergent fronto-temporo-parietal network given the conceptual differences between the measures. The word-level measure (content word quantity) was agnostic to the context of the event or larger narrative, but that information directly informed the event-level measure (subjective ratings). The latter was sensitive to both the local context, in that ratings were given to events segmented based on the progression of the narrative, and the global context, in that ratings were given consecutively allowing for prior information to impact perception of the event. It is thus notable that the word and event semantic content predictors engage a highly similar network given the impact of context on conceptual representations (Yee & Thompson-Schill, 2016). Conceptually and practically, both measures were strongly impacted by the total number of words, which was evidenced by the moderate-to-high correlations between number of words and semantic event ratings across movies. In naturalistic communication, especially in scripted narratives, semantic content is inherently related to verbal input (though they are not identical: semantic ratings also captured narrative moments with non-spoken information or moments in which highly important information is conveyed using few words). Statistically removing that association would create minimally interpretable event ratings; a different approach

is needed for studying naturalistic semantic processing independent of verbal processing. For the present study, a more useful approach is to consider the word-level and event-level results together, noting their similarities and differences.

There were minor differences in the topography of the word-level and event-level semantic content networks. The semantic event network engaged a larger cluster in left inferior frontal gyrus and supplementary motor area, as well precuneus, middle cingulate cortex and surrounding subcortical structures (putamen, thalamus, caudate nucleus), and left inferior and middle occipital gyrus. This may reflect differences in word versus event processing. For instance, the occipital activation observed for highly semantic events is consistent with the fact that linguistic content could be presented via spoken or written language. In addition, differences in temporal receptive windows drive regional recruitment in response to word, sentence, or paragraph presentation (Lerner et al., 2011). The latter two contexts engage a large left inferior frontal region as well as posterior cingulate and precuneus, which we similarly observe in the network that co-varies with highly semantic event content. Processing movie events, which incorporate context in much the same way as sentences or paragraphs, could then drive engagement of regions which allow preceding context to have a greater influence on the integration of information. In addition or alternatively, event content ratings may have been influenced by other types of information (e.g., emotional information), so the resulting network of regions may reflect sensitivity to both semantic and correlated information.

In a recent study using similar word-level predictors but with an audiobook stimulus, engagement of the same lateral portion of ATL was not observed in response to an increase in the quantity of content words (Thye et al., 2023). Instead, the temporal pole, including ventrolateral ATL, was active when there was a decrease in content words. This was thought to be driven by the fact that the speech rate, and therefore approximate quantity of words, tends to be fairly consistent throughout an audiobook. The ventrolateral ATL then is still engaged in semantic processing and may use the relative decrease in new, plot-progressing information to integrate the current information with the prior knowledge of the narrative. This is not the case for movies, which can have periods that are primarily (or entirely) visual, when minimal verbal information is presented. Both studies used a parametric modulation approach, but in the audiobook context, the ‘low semantic’ condition still

contained words (predominately closed class words) whereas the same condition in the present study likely contained no words at all (scenes with only visual information). In measuring regional covariation in response to high relative to low semantic content, it appears that ATL activation does not selectively co-vary with an increase in content words in the audiobook case where the speech rate is consistent even for the low semantic periods. Conversely, in the movie case where ‘low semantic’ means limited to no verbal input, we see ATL activation co-vary with an increase in semantic content. This may indicate important differences in how unimodal (e.g., audiobook) and multimodal (e.g., movie) narratives engage the same cognitive system, which needs to be considered when defining research questions or adapting paradigms. Anticipating this difference between audiobooks and movies, for instance, the present study used summed factor scores instead of mean factor scores to better capture the total amount of each content type. Using means instead of sums appears to better approximate the relative amount of these properties when the speech rate is consistent, as in the audiobook case.

We speculate that ventrolateral ATL, in particular the anterior middle temporal gyrus, is engaged by internal, or endogenous, semantic processing required for updating and processing the ongoing narrative. With a longer temporal receptive window for accumulating and integrating information (Hasson et al., 2008; Lerner et al., 2011) and with functional connections to the broader default mode network (DMN) (Lee et al., 2020; Raichle, 2015), this region is well-suited to serving this role. The DMN, which is active in the presence and absence of external input, facilitates the construction of a continuous coherent internal narrative by relying on episodic and semantic memory (Menon, 2023). This is observed across naturalistic comprehension contexts. Intact story comprehension elicits robust, cross-subject stimulus-induced changes in connectivity between the posterior cingulate cortex, a core DMN region, and anterior MTG (Simony et al., 2016), and activation in the DMN covaries with high-level perception of narrative features during movie-viewing (Betti et al., 2013; Brandman et al., 2021). We suggest that functional connections between the default mode network and ventrolateral ATL drive narrative integration and support endogenous semantic processing of the narrative content. The endogenous processing demands placed on this region are poorly approximated by the relative amount of semantic input. Instead, the dorsolateral ATL appears to be

particularly sensitive to the quantity and informativeness of the input as evidenced by greater activation in this region in both word and event results of the present study and in the universal language network.

### *4.3 Semantic Flexibility*

Counter to our pre-registered hypothesis, there was no evidence of increased engagement of semantic control network regions as semantically flexible word-level content increased. This suggests that processing words with positive Semantic Flexibility scores, which are associated with more frequent, less concrete, and more semantically diverse language, does not require more semantic control. We expected words with high semantic diversity to place additional demands on the control system due to the need to select from one of several possible meanings that best fit the context (Hoffman et al., 2013). This prediction was based on prior studies, which tended to use highly decontextualized stimuli in which meaning selection did not benefit from the context provided in a narrative. During naturalistic language comprehension, highly semantically diverse language appears to be disambiguated by the preceding context without requiring engagement of the semantic control system. These results suggest important deviations from single-word and sentence level investigations of semantic diversity and ambiguity resolution more generally. Similar to the present study, an increase in bilateral parietal and occipital activation was observed in a previous study as positive Semantic Flexibility scores increased (Thye et al., 2023).

### *4.4 Social content*

Recent evidence suggests that social knowledge is subsumed within the semantic system and, like other types of semantic information, is processed in the ventrolateral ATL (Balgova et al., 2022; Binney & Ramsey, 2020). In this view, all kinds of social knowledge are processed within the semantic system, ranging from social concepts, which have consistently been shown to recruit portions of left ATL (Binney et al., 2016; Olson et al., 2013; Zahn et al., 2007), to more abstract social processes such as mentalizing, which have not been as thoroughly investigated (but see Balgova et al., 2022). The present study enabled a direct test of this claim using

naturalistic movie stimuli, which better approximate real-world socio-cognitive processing, across two social contexts: (1) social words, estimated using Social Impact factor scores, and (2) social events, using subjective event-level ratings. We hypothesized that the social network shown in **Figure 1** would be engaged by both content types, in particular within the core regions highlighted in the figure. The results provide partial support for this claim.

An increase in highly social and emotionally arousing words engaged much of the social cognition network: dorsomedial prefrontal cortex, bilateral IFG, superior frontal gyrus, supramarginal gyrus, precuneus, bilateral ATL, and left IPL, with minimal engagement of bilateral MTG. These results broadly align with the pre-registered predictions, and are similar to the regions identified in separate meta-analyses of social compared to non-social concepts (Arioli et al., 2020; Zhang et al., 2021). Unexpectedly, however, activation in left IPL did not co-vary with an increase in Social Impact. In addition to the core social cognition regions, an increase in word-level social content co-varied with activation in precentral and postcentral gyri, middle cingulate cortex, and left inferior occipital gyrus. Activation in ventrolateral ATL co-varied with an increase in social and emotional language. This provides critical support for the claim that social processing is supported by the semantic system (Binney & Ramsey, 2020), but it is important to consider the nature of the contrast. The predictor in this analysis was the socialness of the words, with the quantity of semantic content statistically controlled by using residual scores, so the analysis should not identify regions that are responsive to general semantic or language comprehension. That is, if activation of ventrolateral ATL is primarily driven by the amount of semantic content, then it should not co-vary with Social Impact after controlling for semantic content.

If ventrolateral ATL activation during periods of high Social Impact cannot be attributed to an increase in general semantic content, what is driving this effect? Engagement of this region for processing social relative to non-social word-level content may suggest an increased sensitivity to social information, at least in naturalistic contexts. Alternatively, and building upon our claim about ventrolateral ATL, word-level social processing may drive greater engagement of ventrolateral ATL due to a greater need for endogenous semantic processing. This may be a consequence of the general role of the DMN in social processing (Li et al., 2014) or

may be due to the nature of movies in which social information is particularly salient and important to the narrative.

Although the word-level analysis used orthogonalized factor scores, a ‘pure’ social factor did not emerge from the PCA. Instead the Social Impact factor was driven by socialness and emotional arousal, making it hard to disentangle the social versus emotional effects. In complex, naturalistic stimuli, however, social and emotional content are likely to be at least moderately correlated. Highly social moments are often emotional, and, inversely, emotional moments may frequently be played out between characters, given the likely oversampling of social content in compelling storytelling. Further, conceptual representations are not static (Yee & Thompson-Schill, 2016), but the word-level predictor treated the words as independently sampled from the narrative, a limitation that the event-level predictor directly addressed.

In accounting for the impact of context on conceptual representations, the event-level analysis may have better captured the kind of socio-cognitive processing typically isolated in studies of social cognition. Although social event ratings were moderately correlated with word quantity, the social event predictor also captured non-linguistic content, as intended. Highly interpersonal moments in a movie may contain few, if any, words, and are separate from the linguistic content present in the event. Conceptually, the word and event predictors could capture different properties of the underlying stimulus, although prior work looking at the correspondence between word-level and passage level emotion ratings suggests otherwise (Bestgen, 1992).

Highly social events engaged a network that only partially overlapped with the word-level social content network and included different core social cognition regions. Activation along bilateral superior temporal gyrus extending posteriorly into bilateral lateral occipitotemporal cortex and left angular gyrus co-varied with the social content in events. Processing dynamic social events appears to engage motion processing areas in middle temporal visual motion area (MT), face and object recognition areas in the lateral occipital cortex, and superior temporal sulcus, which may aid in face and body perception (Born & Bradley, 2005; Grill-Spector et al., 2001; Nagy et al., 2012; Pitcher & Ungerleider, 2021). The ATL was not recruited during social event processing, providing counterevidence against the claim that

general social processing recruits the domain-general semantic hub (Balgova et al., 2022). However, it may be that ventrolateral ATL was equally engaged by highly and weakly social events, and, unlike the word-level results, did not evidence increased sensitivity to social events.

The overlap between the social and semantic control system has been interpreted to suggest that socio-cognitive processing places increased demands on the semantic control system (Binney et al., 2016; Diveica et al., 2021). Support for this claim in the present study is mixed. Words that were more social and emotionally arousing (i.e., higher Social Impact) engaged the semantic control network in bilateral inferior frontal gyri, but this was not observed for highly social events. An important consideration in weighing the evidence is the degree to which the word and event-level predictors may have had different control demands that are hard to quantify in naturalistic stimuli. Alternatively, social event-level information may be more readily understood than word-level information. This inference is not without precedent. Many social phenomena studied out of context have been shown to increase general control demands. Processing embedded mental states (e.g., Marty *understands* that Doc *believes* that reading the letter would change the future), for instance, is effortful in a sentence or passage context (Lewis et al., 2017; Stiller & Dunbar, 2007), but is readily understood, and even enjoyable, in the narrative context (Van Duijn et al., 2015). Humans process information well when presented in narrative format (Bruner, 1986), which movies provide. Socio-cognitive processing may engage the semantic control system in experimental paradigms that present de-contextualised stimuli in a random order, but not in a rich narrative context or during naturalistic social processing. Taken together, we do not find strong support for the claim that socio-cognitive processing increases semantic control demands. Prior studies isolating specific social processes that found support for this claim are challenged by the ease with which humans engage in these processes in naturalistic contexts.

#### 4.5 Shared processing

One of our study aims was to investigate the consistency of subject-level engagement of semantic and semantic control networks in processing social concepts. The distribution of subject-level overlap, quantified using number of voxels

and Dice Similarity Coefficient (**Figure 7**), suggested that cross-system overlap exists, but its location was highly variable across subjects and the median values tended to be modest. Taken together, these results provide minimal support for a consistent locus of overlap between these cognitive systems.

## 5 Conclusion

Naturalistic neuroimaging data provide an exciting and rich basis for studying the neural basis of human cognition. However, this richness also makes them particularly vulnerable to adjusting analysis strategies and constructing post hoc explanations, which is common in whole-brain neuroimaging. The analyses and hypotheses described in the present study were based on well-defined theories of semantic and social cognition (and how they might interact) and pre-registered to maximize transparency about the analysis plan (and any deviations) and distinguish *a priori* hypotheses from post hoc speculations based on the results.

The results suggest that during naturalistic movie viewing, increases in semantic content are associated with increased activation in the semantic and semantic control networks, displaying a fronto-temporo-parietal topography highly similar to the universal language network (Malik-Moraleda et al., 2022). There is evidence of a hub architecture, consistent with the graded hub hypothesis (Lambon Ralph et al., 2017), but the ATL subregions appear to serve different functions during naturalistic comprehension. We suggest that the dorsolateral ATL is sensitive to the quantity and informativeness of the input, as evidenced by robust activation during language comprehension, whereas the lateral portion of ventrolateral ATL may be also important for endogenous semantic processing – updating and processing the ongoing narrative – leveraging this region’s functional connections with the default mode network. Word, but not event-level, social content engaged the ventrolateral ATL, perhaps because social content is particularly important for movie narratives and consistent with the role of this region in endogenous semantic processing. Social events engaged a network topographically more similar to the social cognition network, with activation in bilateral TPJ. Although portions of the semantic network (ATL, right IPL) were engaged by social content and these regions overlapped at the group level, the subject-level overlap analyses suggest limited cross-subject overlap. These results are a step toward integrating theories of word-level semantic cognition

with theories of narrative comprehension and understanding the relationships between social and semantic cognition.

# **Chapter 6**

## **GENERAL DISCUSSION**

### **1 Overview**

Semantic memory provides a conceptual store that is critical for language comprehension – we use this knowledge to flexibly communicate complex ideas and convey rich, nuanced information through natural language and narratives (McRae & Jones, 2013). In most cases, the process of rapidly accessing and integrating the meaning of individual concepts into a holistic representation is done with ease, despite the multifaceted cognitive demands required for successful comprehension. These demands have been underestimated by the prevailing hub-and-spoke model of semantic cognition, which was developed using highly constrained stimuli that poorly approximate real-world language processing. Further, there is evidence that the semantic system facilitates social processing (Balgova et al., 2022; Binney & Ramsey, 2020), but this claim has not been tested using naturalistic stimuli that sample varied social knowledge, including abstract social concepts, pragmatic inferences, and interpersonal interactions.

The aims of this thesis were broadly two-fold: (1) to examine the neural processing of semantic information across comprehension contexts, and (2) to investigate comprehension of social information in narratives, particularly the engagement of semantic and social systems. These aims were tested by examining the neural processing of different kinds of relations between concrete concepts (i.e., taxonomic and thematic relations – [Chapter 2](#)), abstract lexical and semantic properties of single words presented in context in an audiobook ([Chapter 3](#)), social and pragmatic sentence content in the same audiobook ([Chapter 4](#)), and social and semantic word and event level ratings in multimodal movies ([Chapter 5](#)). This forms the basis for extending the hub-and-spoke model of semantic cognition to narrative comprehension contexts and for a better understanding of how social information is processed within the neural architecture of the semantic system.

## 2 Cross-cutting implications

Across the studies described here, we observed important deviations from the hub-and-spoke model. Prior studies that used natural language or narratives to probe the neural basis of the semantic system foreshadowed differences in the neurobiology of language processing (Deniz et al., 2019; Huth et al., 2012, 2016), but our results suggest that the neural architecture described by the hub-and-spoke model may not sufficiently capture the temporal processing of concrete semantic relations. Chapter 2 provided evidence of a dual-hub structure, with specialization for taxonomic, or feature-based relations, in ATL and for thematic, or event-based relations, in IPL. This specialization was time sensitive and likely too transient for fMRI studies to capture given the relatively sluggish BOLD response.

Chapters 3 and 4 investigated a complete narrative, *The Little Prince*, using two complementary levels of analysis: word properties of the sort that informed the hub-and-spoke model and sentence ratings that explicitly integrated narrative context. Chapter 5 described an application of an analogous word-level approach to movie stimuli and extended the prior work by incorporating more context via event ratings. Across these three studies, we observed engagement of large, bilateral networks, particularly for processing word quantity and semantic content. Social language, including pragmatic inference, engaged the semantic system in ATL, but this was not observed for social events. Consistent with the hub-and-spoke model, there was evidence of a hub architecture, but we identified three subregions within the ATL that appear to be differentially functionally engaged by the varying demands of narrative comprehension (**Table 1**). Several cross-cutting inferences can be made in light of these results, outlined in the sections below.

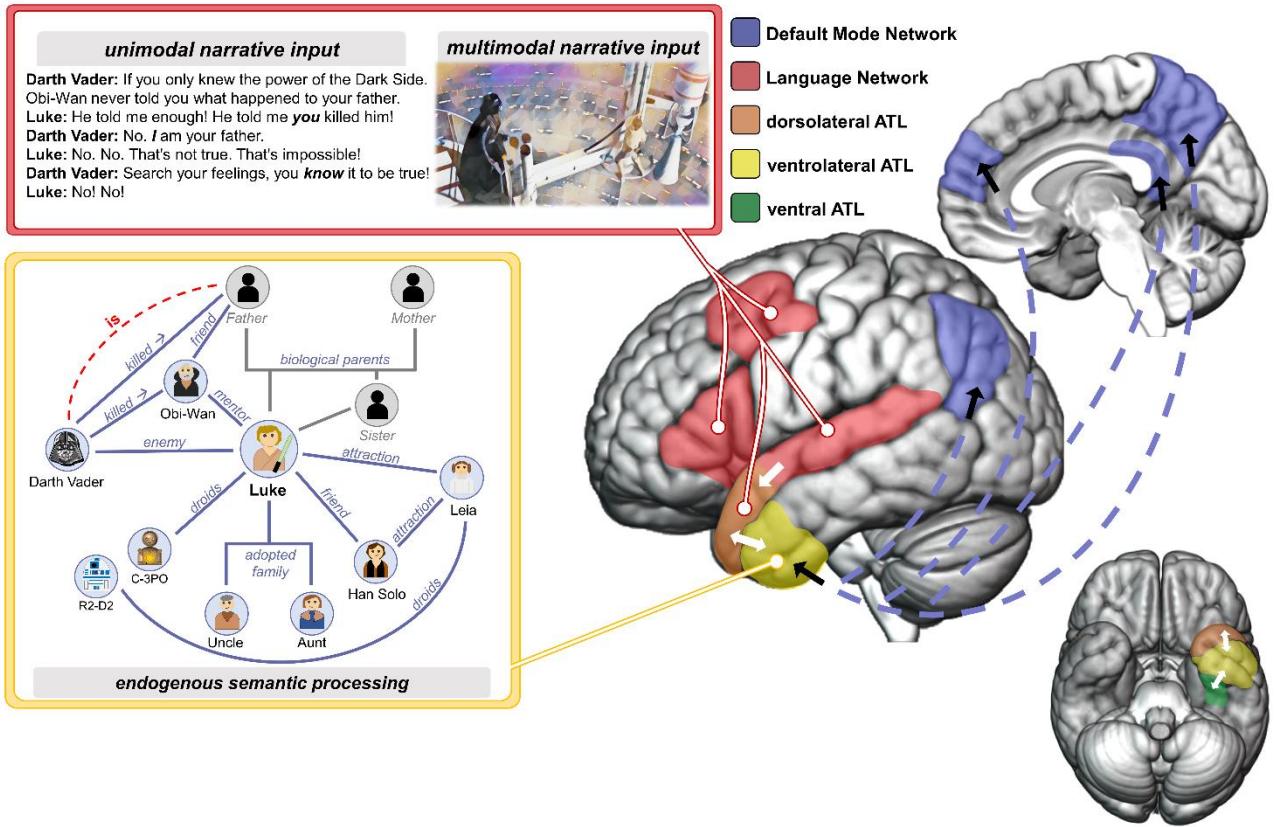
**Table 1***ATL functional subregions*

<b>Subregion Label Anatomical Boundaries</b>	<b>Proposed Sensitivity</b>	<b>Evidence</b>
<b>Dorsolateral ATL anterior STG</b>	quantity of verbal / semantic input	<p><b>Ch 3: audiobook words</b></p> <ul style="list-style-type: none"> <li>• activity correlates with number of words*</li> </ul> <p><b>Ch 4: audiobook sentences</b></p> <ul style="list-style-type: none"> <li>• activity correlates with semantic content ratings</li> </ul> <p><b>Ch 5: movie words &amp; events</b></p> <ul style="list-style-type: none"> <li>• activity correlates with number of content words &amp; semantic event ratings</li> </ul> <p><b>Universal language network (Malik-Moraleda et al., 2022)</b></p>
<b>Ventrolateral ATL anterior MTG &amp; ITG</b>	(1) social words and sentences and sentences requiring pragmatic inference  (2) narrative moments with minimal verbal / semantic input	<p><b>Ch 3: audiobook words</b></p> <ul style="list-style-type: none"> <li>• activity correlates with Social Impact scores*</li> </ul> <p><b>Ch 3: audiobook words</b></p> <ul style="list-style-type: none"> <li>• activity negatively correlates with number of content words*</li> </ul> <p><b>Ch 4: audiobook sentences</b></p> <ul style="list-style-type: none"> <li>• activity correlates with social* and pragmatic content ratings</li> </ul> <p><b>Ch 5: movie words</b></p> <ul style="list-style-type: none"> <li>• activity correlates with Social Impact scores</li> </ul>
<b>Ventral ATL anterior fusiform</b>	general semantic content	<p><b>Ch 3: audiobook words</b></p> <ul style="list-style-type: none"> <li>• activity correlates with number of content words</li> </ul> <p><b>Ch 4: audiobook sentences</b></p> <ul style="list-style-type: none"> <li>• activity correlates with semantic content ratings</li> </ul> <p><b>Role as transmodal semantic hub (Lambon Ralph et al., 2017)</b></p>

Note. ATL, anterior temporal lobe; STG, superior temporal gyrus; MTG, middle temporal gyrus; ITG, inferior temporal gyrus. The subregions are shown in **Figure 1**. \*activation in dorsolateral and ventrolateral ATL

## *2.1 Endogenous semantic processing framework*

The studies presented here provide the basis for a model of narrative comprehension that integrates the perisylvian language comprehension network, the hub-and-spoke semantic cognition system, and the default mode network (DMN). In this model, unimodal or multimodal narrative language input is processed within the language and semantic networks, including dorsolateral ATL (anterior STG) and the semantic hub in ventral ATL (anterior fusiform). Internal processing or reflection on the narrative and updating of the situation model or narrative schema is supported by the DMN and also requires semantic cognition – we refer to this as “endogenous semantic processing” to indicate semantic cognition that is driven by internal factors rather than external input. We suggest the ventrolateral ATL plays a critical role in endogenous semantic processing and mediates between the DMN and the semantic and language networks. The proposed model is depicted in **Figure 1**, and the key features of the model are described below.



**Figure 1. Proposed model for the neural basis of narrative comprehension.** The default mode network (purple), the language network (red), dorsolateral ATL (orange), ventrolateral ATL (yellow), and ventral ATL (green) are shown on the left lateral, inferior, and medial surface of the brain. The top panel outlined in red provides example unimodal (auditory or visual) and multimodal narrative input. Outlined red lines connect this input panel to the language network including dorsolateral ATL, demonstrating the proposed network engaged by external input during narrative comprehension. The bottom panel outlined in yellow shows a schematic of the evolving situation model in response to the narrative input. Within this panel, purple lines indicate information that was known prior to the scene, grey lines indicate information that is unknown, and the red dashed line indicates the new connection formed after the input is processed. An outlined yellow line connects this bottom panel to the ventrolateral ATL, demonstrating the proposed endogenous processing this region supports. Dashed purple lines flow between the ventrolateral ATL and regions within the default mode network, demonstrating the proposed functional connections that facilitate the endogenous processing. White arrows overlaid on the language network and dorsolateral ATL show the flow of input processing accessing semantic memory in the dorsolateral ATL. Bidirectional white

arrows connect dorsolateral and ventrolateral ATL and ventrolateral and ventral ATL demonstrating that the functional boundaries between these regions is not rigid. Multimodal narrative input is likely to engage regions not depicted in the figure. For instance, visual input may feed into and facilitate endogenous semantic processing. To simplify the presentation of the proposed model, however, we have highlighted only the regions the framework makes specific claims about.

*There is a robust language comprehension network that includes dorsolateral ATL*

There is a robust fronto-temporo-parietal language comprehension network that includes left inferior frontal gyrus, middle frontal gyrus, and superior temporal gyrus extending anteriorly into dorsolateral ATL. This network topography is highly convergent with the universal language network, as discussed in Chapters 4 and 5. Activation in ventrolateral ATL was notably inconsistent – only about a third of the language network maps in the Malik-Moraleda et al (2022) study appeared to include ventrolateral ATL whereas all of the network maps included dorsolateral ATL. The topography of this network may be particularly driven by auditory input and, given its proximity to auditory cortices, dorsolateral ATL may be ideally positioned to support auditory language comprehension. In the present studies, semantic word and event-level content consistently engaged dorsolateral ATL and, less consistently, extended into a portion of ventrolateral ATL. Ventral ATL may be particularly sensitive to an increase in semantic word and sentence level content, but it was not engaged during multimodal word or event content.

We suggest that, within ATL, the dorsolateral subregion, alongside this broader language comprehension network, is particularly engaged by linguistic input. This claim runs counter to what some studies of the semantic system suggest, indicating instead that dorsolateral ATL is sensitive to social processing (Olson et al., 2013; Zahn et al., 2007). In studies where the contrast was between a story (*Alice in Wonderland*) and acoustically degraded audio or unfamiliar language (e.g., Malik-Moraleda et al., 2022), both language and social content were present in the story condition and absent in the control condition. The present studies, however, explicitly controlled for social content at the word, sentence, and event levels and still observed a highly convergent comprehension network that included dorsolateral ATL. Further, activation within these language network regions, including

dorsolateral ATL, parametrically increases with the length of sentences (Pallier et al., 2011), and the same network is engaged for minimally social, descriptive texts. In the latter case, non-social narrative input is processed indiscriminately within this network regardless of coherency: the network is equally engaged by coherent narratives and an equal number of unconnected sentences (Jacoby & Fedorenko, 2020). Importantly, this network topography is not observed for unintelligible language or scrambled words and only starts to emerge when the coherent input is on the sentence timescale (Lerner et al., 2011). This demonstrates two key points. First, the integration timescale of these regions appears to approximately plateau at the sentence-level, restricting how much meaning is accumulated and integrated. Second, this underscores the preferential role this network plays in processing linguistic input and suggests that integration of the meaningful discourse-level information, which is only possible in the coherent narrative condition, happens at least partially outwith this language comprehension network.

It is likely that studies using simple isolated stimuli would not be sensitive to detecting this effect. In these studies, by design, the linguistic input is constrained by the simplicity of the stimuli. In addition, the linguistic input is likely to be approximately balanced between conditions – for example, a contrast between single words or word-pairs that differ on a single dimension but are matched on other relevant psycholinguistic properties. Where narrative stimuli present linguistic information in context, accruing meaning over time, paradigms that restrict this information by presenting unconnected words or sentences in random order, limit the amount of information that requires integration. These paradigms have been, and will continue to be, critical for answering questions about the neurobiology of human cognition, but they necessarily miss some of the real-world demands placed on the cognitive system. This property of the dorsolateral ATL may have been missed in prior research for this reason: the stimuli placed minimal (and matched) input demands on the semantic system.

#### *Narratives place internal processing demands on the semantic system*

Comprehending words in a narrative requires both retrieving the word-level meanings and integrating them with the preceding content. The comprehender must continually update their situation model of the ongoing events (Yarkoni et al., 2008;

Zwaan, 2004; Zwaan & Radvansky, 1998). Rapidly retrieving incoming conceptual representations and holding a mental representation of an extended, coherent narrative or conversation places different demands on the semantic system than individual concepts presented in isolation, devoid of any context.

The process of updating situation models is thought to be primarily supported by the default mode network (DMN) (Tylén et al., 2015; Yeshurun et al., 2021), and the properties of this network suggest that it is ideally situated to interface with semantic (and other) cognitive systems to enable online comprehension. The seven functional connectivity networks of the brain (Yeo et al., 2011) can be organized along a principal gradient, with the DMN existing at one extreme and sensory and motor networks at the other (Margulies et al., 2016). This topographical organization indicates that DMN serves as transmodal cortex, situated at a confluence of sensorimotor and memory input streams, playing an active role in context-dependent processing of rich, naturalistic stimuli. This is particularly true of context arising from semantic information or associations in comparison to other types of information (i.e., letter symbols) (Smith et al., 2021). Indeed, functional connections between posterior DMN regions (e.g., posterior cingulate and precuneus) and lateral ATL, particularly the ventrolateral region, and posterior middle temporal gyrus, may facilitate this process. Through these connections, the DMN can interface with semantic memory, updating a cumulative situation model by integrating semantic representations into coherent context (Smallwood et al., 2016). This is observed in the preferential sensitivity of DMN regions to semantic content over quantity of input alone. Coherent, semantically rich narratives drive intersubject synchronization in connectivity in DMN regions, and narratives activate DMN regions, a pattern not observed for less semantically complex scrambled input (Lee et al., 2020; Lerner et al., 2011). In integrating this prior research with the results of empirical chapters presented in this thesis, we suggest that the semantic system interfaces with the default mode network to internally process the conceptual information in the narrative.

### *Ventrolateral ATL supports endogenous semantic processing*

In a narrative, new words and sentences are not just semantic blocks to be added to a growing pile of information. New information deepens and changes the understanding of preceding information (as illustrated in **Figure 1**), a process that also requires semantic cognition independent of comprehending the most recently presented word or phrase. Updating, restructuring, and reflecting on the situation model is what we call “endogenous semantic processing”, and our results indicate that ventrolateral ATL supports these processes during narrative comprehension.

This interpretation is based on integrating evidence from the present studies of narrative comprehension with prior work on processing single concepts.

Ventrolateral ATL is consistently found to be more responsive to semantic than non-semantic demands, i.e., it is part of the semantic hub (Lambon Ralph et al., 2017). In the present studies, we find that dorsolateral and ventral ATL are consistently parametrically more responsive to quantity of semantic input (i.e., stronger response when there is more semantic input), but ventrolateral ATL does not show this pattern. In single-concept studies, by design, there is an isolated semantic-vs-non-semantic contrast and ventrolateral ATL is sensitive to this contrast because it is part of the semantic hub. However, in a narrative context, there are always endogenous semantic processing demands, which drive ventrolateral ATL activation even when semantic input is low (unlike dorsolateral and ventral ATL, which are specifically sensitive to quantity of semantic input). This is most evident in the results of Chapter 3 in which activation in the DMN and the ATL positively co-varied with a *decrease* in semantic content. Although these results include both the dorsolateral and ventrolateral ATL subregions (but not the ventral portion) making the functional differences indistinguishable, they can be explained by engagement in endogenous semantic processing. During moments when the semantic input is light – narrative moments comprised of predominately closed class words – the input demands are minimized (but not absent which might explain engagement of dorsolateral ATL, but not the rest of the language comprehension network). The listener, having a moment of relative lull in a fast-paced narrative, is then able to engage in endogenous semantic processing via activation of the default mode network and lateral ATL. In the absence of endogenous semantic processing demands (e.g., single-concept studies), ventrolateral ATL is sensitive to semantic input; but in a narrative context,

relatively constant endogenous semantic processing demands produce relatively constant engagement of ventrolateral ATL, so it is not sensitive to differences in semantic input.

The functional role of ventrolateral ATL during narrative comprehension emerges when the present studies are considered in tandem. As discussed above, dorsolateral and ventrolateral subregions were both engaged during narrative moments with reduced semantic input in Chapter 3. Both regions were also engaged alongside the posterior extent of superior temporal gyrus during narrative moments with increased linguistic input (i.e., number of words). The sensitivity of these subregions becomes clearer when the results of Chapter 4 and Chapter 5 are considered. In Chapter 4, by contrasting high semantic sentences with low semantic sentences in the same narrative, we observe an extensive comprehension network that includes dorsolateral ATL and some of ventrolateral ATL, but not the anterior segment. When the same predictor (number of content words) is considered in movies, we similarly observe robust activation in dorsolateral ATL and only a small portion of ventrolateral ATL. The comprehension context matters here: in the audiobook case, words – largely semantically light words – are still consistently presented during “low semantic” narrative moments. In the movie case, the linguistic input is likely minimal if not absent in the “low semantic” narrative moments because movies can rely on other modalities to engage the viewer. The balance of input and internal processing demands is then not equally matched for the same predictors estimated for audiobooks (or unimodal narratives) and movies (or multimodal narratives). When the input demands are better approximated by the predictor – semantic sentence content in Chapter 4 and semantic word and event content in Chapter 5 – the analysis isolates the functional subregion within ATL that preferentially responds to linguistic and semantic input: the dorsolateral ATL. When the input demands are approximately matched between conditions and what differs is content that is a particularly strong driver of internal semantic processing – social and pragmatic sentences in Chapter 4 and social words in movies in Chapter 5 – the analysis instead isolates the subregion that is preferentially sensitive to endogenous processing: ventrolateral ATL.

In summary, ATL subregions appear to have complementary roles during narrative comprehension: dorsolateral and ventral ATL are sensitive to the amount of

linguistic or semantic input, respectively, whereas ventrolateral ATL is sensitive to content that drives internal processing and integration with the ongoing situation model.

## 2.2 Evidence of social processing in the semantic system

Social language (words and sentences) consistently engaged the semantic system in left ATL, predominately in ventrolateral ATL. This was true both for literal social language and for language that required social reasoning beyond the literal concepts in the sentence – pragmatic inference. These results are consistent with the claim that social processing leverages semantic memory and its neural architecture (Binney & Ramsey, 2020). However, the claim that social processing leverages semantic cognition systems does not explain why ventrolateral ATL was engaged *more* by social compared to non-social language.

Evidence of sensitivity to social information in ventrolateral ATL has been inconsistent. Some prior studies have found that dorsolateral ATL is particularly sensitive to social information (Olson et al., 2013; Zahn et al., 2007), whereas others predominately observe activation in ventrolateral ATL (Balgova et al., 2022; Binney et al., 2016). Engagement of both subregions was similarly observed in a subset of the present studies. An increase in social words and sentences in Chapter 3 and 4, respectively, was associated with activation in both regions. The ventrolateral ATL was the *most* consistently engaged region across the studies presented here, however, and the results were more localized to ventrolateral ATL (and not dorsolateral ATL) when highly pragmatic sentences and social words in movies (Chapter 5) were considered. In these analyses, quantity of semantic input was controlled (statistically in parametric analyses in Chapters 3 and 5, and by matching sentences in Chapter 4), so this is again inconsistent with ventrolateral ATL being purely sensitive to semantic input processing demands. This is perhaps easiest to see in the condition contrasts in Chapter 4 (**Table 2**): there was an approximately equal distribution of high, moderate, and low semantic sentences in the high and low social and pragmatic conditions. Therefore, the semantic input demands of high and low social and pragmatic content sentences were matched and should be subtracted out in the contrasts. In line with this, we did not observe activation in the ventral ATL hub and activation in the dorsolateral region was minimal, especially in the pragmatic

case. This is consistent with the results of a prior study in which theory of mind paradigms, including those with minimal semantic input demands, primarily engage the ventrolateral ATL and not the dorsolateral or ventral ATL subregions (Balgova et al., 2022). A simple explanation is that the ventrolateral ATL is domain-specific and specialized for social information processing. However, there is a preponderance of evidence from neuropsychological, computational, and neuroimaging studies that support the role of ventrolateral ATL in general, non-social semantic processing (Binney et al., 2010; Chen et al., 2017; Lambon Ralph et al., 2010, 2012, 2017). Therefore, the domain-specific explanation can be rejected.

**Table 2**

*Example contrast predictions and results*

Condition	Semantic	Social	Dorsolateral	Ventrolateral	Ventral
Social High		✓			
Social Low	matched	✗	X	X	
Pragmatic High		✓			
Pragmatic Low	matched	✗		X	
Semantic High	✓				
Semantic Low	✗	matched	X		X

Note. This table refers to the contrasts (High > Low) used in [Chapter 4](#). The stimuli were sentences extracted from a coherent narrative that differed in content type – social, pragmatic, and semantic content are used in this example.

The endogenous semantic processing framework provides an alternative explanation: social information, especially pragmatic inference, drives endogenous semantic processing particularly strongly. That is, new social information prompts more reflection and updating of the situation model than non-social information does. As a result, ventrolateral ATL response to social information reflects greater engagement of endogenous semantic processing rather than intrinsic sensitivity to processing social information in particular. Similarly, pragmatic inference requires using narrative context to interpret sentences in a non-literal way – another form of endogenous semantic processing. In other words, social and pragmatic content in narratives requires semantic input processing like any other kind of semantic input, and particularly strongly drives internal processing, at least when comprehending

highly social narratives (such as the audiobook and movies used here). The example narrative provided in **Figure 1** demonstrates this point. Audiobooks and movies generally introduce a host of characters who interact with each other and the protagonist (in this case, Luke) in nuanced and evolving ways. The event depicted in the figure is an exchange between only two of the characters, but – in addition to comprehending the individual words of dialogue – the information conveyed in the exchange has an immediate, downstream impact on the viewer’s entire situation model, requiring a re-mapping of several character relations. That this particular example is highly social and also requires extensive endogenous semantic processing is a feature, not a bug, of many narratives. We argue that it is *not* the case that ventrolateral ATL is particularly sensitive to social content; instead, this region is engaged in endogenous semantic processing, which social content tends to elicit in many naturalistic language contexts.

Social events were an exception to this pattern, eliciting no ATL activation. It is possible that semantic and social event ratings included the endogenous processing demands more than the word or sentence-level variables did. The event coding protocol, for example, instructed raters to give a high semantic rating to events in which new and plot progressing information is presented to the audience for the first time. This definition may implicitly capture many of those events in which endogenous semantic processing is required – dramatic reveals, plot twists, delivery of critical background information, etc. The event depicted in **Figure 1** would have received a high semantic rating for this reason. At the same time, this event establishes a critical familial relation, which has implications for the identity of the protagonist and encourages reflection of the mental states of the characters in and out of the event, resulting in a high social rating as well. If social content is an oversampled source of endogenous processing in narratives like the ones used here, then the semantic and social ratings are both capturing aspects of that processing. Thus, lack of sensitivity in ventrolateral ATL during social events may have resulted from an analysis strategy that involved controlling for semantic event content.

### *2.3 Domain-general role of IPL in context integration*

Engagement of left inferior parietal lobule (IPL) was observed across the results of the studies presented here. This was a key focus of [Chapter 2](#) which reported specialization in this region for processing thematic relations, or relations that rely on shared context. During narrative comprehension, activation in left IPL co-varied with other lexical and semantic content. In [Chapter 3](#), left IPL was engaged by increases in general linguistic content (i.e., number of words) and social language and a decrease in semantically-laden content (i.e., content words) – providing listeners with a chance to integrate narrative information. A similar pattern emerged in [Chapter 4](#): highly semantic, social, and pragmatic content engaged overlapping portions of left IPL. In [Chapter 5](#), word and event-level semantic content in multimodal narratives engaged IPL, but activation in the region did not co-vary with social content. These results, when considered alongside prior research, indicate that IPL is not domain-specific and instead suggests a possible role in context integration.

A domain-general role for left IPL is noncontroversial, and support for this claim stems from several domains of cognitive neuroscience. The IPL is consistently activated across wide-ranging tasks and is topographically situated at the convergence of several large networks, well-positioned to serve as a cross-modal hub (Igelström & Graziano, 2017; Numssen et al., 2021; Seghier, 2013). Prior evidence of domain specificity may have been driven by a failure to examine evidence across fields. The role of IPL in episodic memory retrieval (Wagner et al., 2005), for instance, is not incompatible with its role in social cognition (Bzdok et al., 2016), action knowledge (Lambon Ralph et al., 2017), and sensorimotor integration (Sereno & Huang, 2014). IPL is a large region, comprised of the supramarginal and angular gyri, and as such is closely functionally connected to the default mode network. In addition, IPL has a long temporal receptive window (Lerner et al., 2011), which facilitates integration of multisensory inputs over a longer timescale.

In line with this evidence, we propose that IPL plays a domain-general role in context integration and memory retrieval of relevant contextual information. This includes thematic relations, which require consideration of shared context, as well as general semantic content and social information, the latter of which aligns with the prior research reporting activation in this region in response to social paradigms. This interpretation is consistent with the endogenous semantic processing

framework outlined above. IPL is proximal to (and part of) the DMN, so it is well-positioned to support not only retrieval of context-relevant semantic and social information, but also its integration into the evolving understanding of the narrative. This further underscores the interdependence between the semantic and default mode networks.

## *2.4 Limitations of Naturalistic Neuroimaging*

The advantages of using narratives, and other naturalistic stimuli more generally, to study cognition have been described throughout this thesis in order to motivate why these paradigms were well-suited to addressing the overall aims of the thesis, but there are several limitations of these approaches that should be noted alongside the inferences drawn from them. Perhaps the most common critique of naturalistic stimuli is the relative loss of experimental control compared to traditional constrained paradigms. The experimental control afforded by traditional approaches allows for orthogonalization between conditions, enabling a strong manipulation of the effect of interest. This is a considerably more challenging task in a narrative stimulus, especially if the condition of interest occurs infrequently. This is exemplified in Chapter 4 by the identification of relatively few syntactically ambiguous sentences within the narrative. The condition effects may also be impacted by the other properties of the stimulus that tend to be oversampled, such as social information (Vanderwal et al., 2019). The extent to which the other properties of the multimodal stimulus might correlate with the property or condition of interest is not always clear or quantifiable, making it hard to disentangle potentially confounded effects. One way to circumvent this problem might be to construct narratives that sample the conditions of interest and provide some experimental control, but this approach was not taken here.

Narrative story-telling is an ancient and ubiquitous part of the human experience, but it is different from interpersonal communication or natural language (Parkinson & Manstead, 1993). This is especially true of passive viewing paradigms which require comprehension, but not active engagement in, the unfolding events and provide limited extrasensory information (e.g., smell, touch) that are likely to impact how social and emotional experiences are processed in everyday life. The narrative events unfold over an artificially rapid timeline relative to events experienced over

the course of a day, year, or lifespan. In addition, comprehending a narrative while undergoing fMRI scanning may better capture language processing compared to the presentation of decontextualized word or sentence stimuli, but it is far from how people engage in language comprehension in everyday life.

An intersecting issue is that, at present, there are no standardized approaches to annotating or analysing naturalistic data. This has ramifications for each stage of the research process. In addition to being time consuming, stimulus annotations can be overfit to the aims and theoretical background of the researcher, and, as such, may be prone to being highly idiosyncratic or difficult to generalize across research fields. A social cognition researcher, for instance, may be attuned to the mentalizing events within the narrative, whereas a semantic cognition researcher might focus on the number of social concepts within an event. This analytic flexibility can be heralded as a strength (Vanderwal et al., 2019), but can also result in parallel analysis streams that ask and answer related questions in highly variable ways, resulting, potentially, in challenges in building towards converging evidence.

Given the unconstrained nature of the stimuli, it is challenging to develop models of cognition from naturalistic paradigms alone (Rust & Movshon, 2005; Saarimäki, 2021). Instead, these paradigms are ideally suited for testing well or partially established models of cognition in more ecologically valid circumstances or in response to situations or processes that are more likely to be influenced by context, such as those investigated in the present thesis. These paradigms offer a promising complement to, rather than a replacement for, the constrained experimental paradigms already employed to great effect in the study of human cognition. Indeed, proponents of naturalistic paradigms openly recognize the value that constrained paradigms have and will continue to provide (Rust & Movshon, 2005; Saarimäki, 2021). The work undertaken in this thesis was designed to strike this balance by testing hypotheses informed by a well-established model of semantic cognition in naturalistic contexts. In doing so, the results can be interpreted with respect to current prevailing theories, enabling cross-cutting inferences of the kind made here.

### **3 Conclusion**

This thesis investigated semantic comprehension across contexts, from word-pairs to multimodal narratives, and across levels of analysis, from single words to sentences and events. The results provide a basis for extending the current neurobiological model of semantic cognition so that it accounts for comprehension in narrative contexts. The model further elaborates on how and why social language engages this system. In doing so, the studies undertaken shed light on how we comprehend the rich language we use in everyday life to communicate complex ideas, explain personal experiences, describe our own and others' emotions and behaviour, and, ultimately, share our human experience with others around us. They further highlight the value and need for naturalistic investigations of the cognitive systems that drive the human experience as it happens once we leave the laboratory.

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## Appendices

### APPENDIX A: CHAPTER 2 SUPPLEMENTAL MATERIALS

**Supplemental Table 1**

*Participant Electrode Coverage*

<i>Participant</i>	<b>ATL</b>	<b>IPL</b>	<b>IFG</b>	<b>pMTG</b>	<b>Total</b>
01	9	4	6	4	23
02	0	0	8	0	8
03	0	0	11	3	14
04	0	0	11	7	18
05	0	8	6	2	16
06	0	0	7	4	11
07	5	0	4	9	18
08	0	3	12	1	16
09	0	0	4	6	10
10	4	6	0	11	21
11	5	3	3	3	14
12	9	0	5	0	14
13	7	1	10	5	23
14	0	0	2	0	2
15	7	0	12	1	20
16	10	0	9	4	23
17	0	0	6	2	8

*Note.* Total refers to the number of electrode channels within one of the regions of interest for each participant. ATL, anterior temporal lobe; IPL, inferior parietal lobule; IFG, inferior frontal gyrus; pMTG, posterior middle temporal gyrus.

**Supplemental Table 2***Task Stimuli*

Taxonomic Pairs (n=16)	Thematic Pairs (n=16)	Unrelated Pairs (n=64)			
ale – cola	blade – armour	alien – scorpion	dune – queen	mountain – chip	spinach – gun
bucket – vase	drizzle – cloud	arrow – tooth	earing – gravy	note – bull	steel – medicine
chicken – owl	forest – trail	balloon – mustard	envelope – lime	pasta – ink	sword – napkin
dentist – surgeon	gown – corsage	block – pilot	foundation – towel	patio – knight	tail – tire
dinner – breakfast	ketchup – burger	bread – chain	gas – magazine	pin – kitty	thorn – fan
jug – urn	light – star	bulb – dog	glove – pretzel	planet – container	thunder – folder
juice – lager	map – route	cable – ocean	grill – pyramid	plantation – pan	toilet – pendant
lamb – cow	monkey – banana	candy – pebble	hair – spatula	plate – basketball	torch – potato
lunch – snack	navy – anchor	canoe – jester	hoop – resume	plug – hat	tricycle – river
otter – rat	padlock – diary	case – web	island – shoe	purse – lobster	viper – stylus
pail – pot	palm – coconut	cave – basket	jackal – sink	reef – building	vulture – page
president – monarch	shovel – sandbox	cheetah – candle	kayak – cheese	rod – mayonnaise	wallet – plant
seal – beaver	soysauce – sushi	computer – radish	lid – crab	rubber – turtle	whiskey – pillow
skunk – rabbit	sugar – tea	cougar – bridge	lightning – cane	salsa – air	wife – football
taxi – airplane	trench – bayonet	cup – weapon	lion – glass	shampoo – cord	wine – grass
yarn – floss	tv – couch	dirt – cake	moth – base	skeleton – flower	yogurt – sail

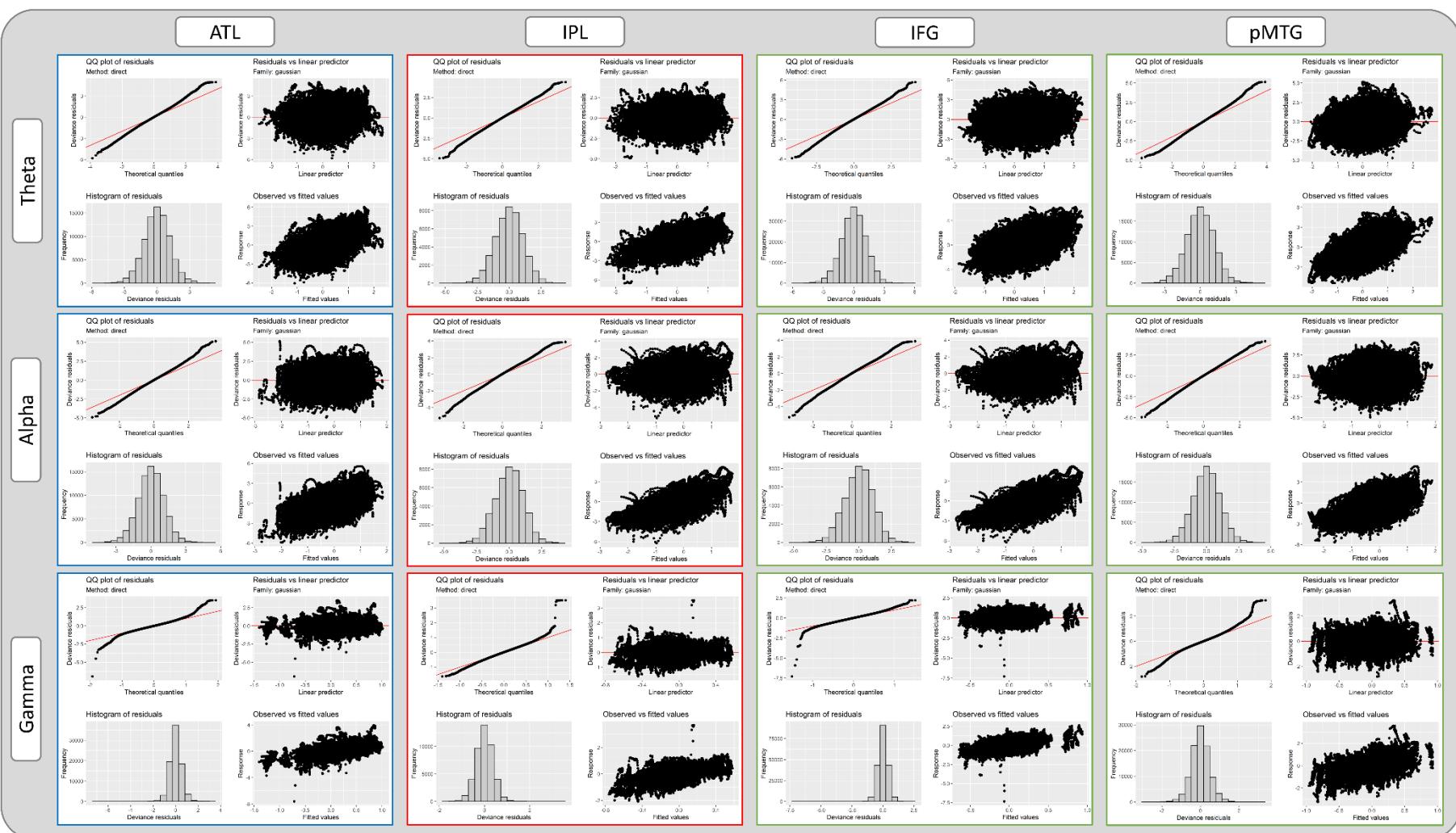
Note. The full task included both strongly (n=32) and weakly (n=32) related taxonomic and thematic word pairs and an equal number of unrelated, filler pairs (n=64). Only the strongly related taxonomic and thematic pairs are shown here. The weakly related pairs are available on the project OSF page, but were not analysed in the present manuscript. All unrelated, filler pairs are listed and shown shaded in grey.

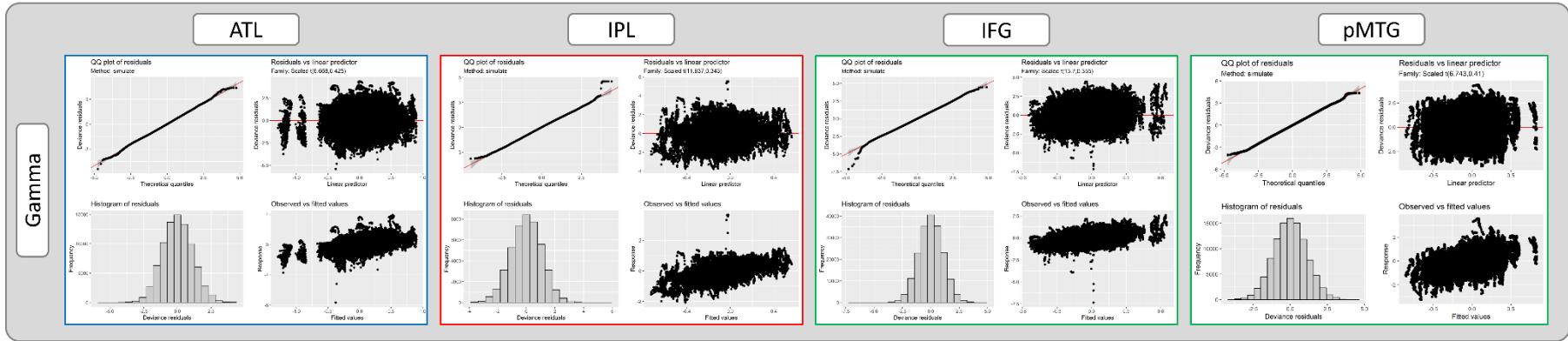
### Supplemental Table 3

#### Model Results

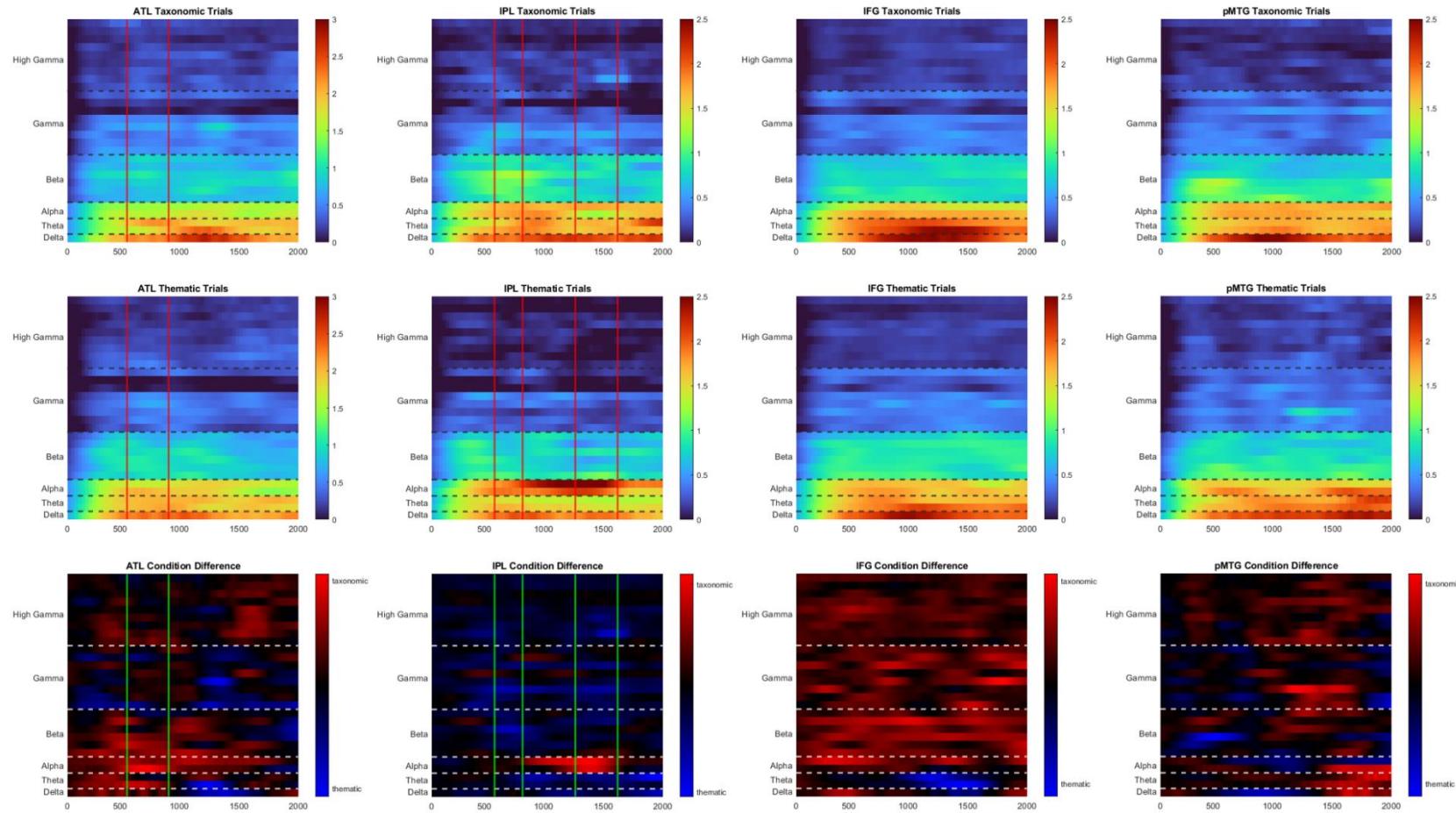
	<b>Trial Type</b> Est(SD); <i>t</i> -value	<b>s(Time)</b> edf(rdf); <i>F</i> -value	<b>s(Time):Them</b> edf(rdf); <i>F</i> -value	<b>s(Time):Tax</b> edf(rdf); <i>F</i> -value	<b>fs(Time, Electrode)</b> edf(rdf); <i>F</i> -value	<b>re(subj_word)</b> edf(rdf); <i>F</i> -value
<b>Theta</b>						
ATL	-0.17(0.10); -1.76†	0.01(0.01); 0.03	6.69(7.49); 2.84**	8.25(8.63); 9.03***	371.66(560); 3.33***	151.40(187); 5.80***
IPL	0.19(0.10); 1.84†	0.00(0.00); 0.00	6.62(7.42); 2.14*	8.61(8.83); 16.42***	154.03(249); 5.12***	108.28(148); 3.80***
IFG	0.09(0.06); 1.64	3.43(3.82); 0.35	6.99(7.75); 3.69**	3.21(3.63); 1.18	808.68(1159); 3.20***	295.29(400); 3.64***
pMTG	-0.01(0.08); -0.08	3.09(3.63); 0.33	1.00(1.01); 2.69	7.50(8.44); 7.16***	461.23(618); 3.82***	254.77(347); 3.64***
<b>Alpha</b>						
ATL	-0.12(0.09); -1.31	2.45(2.57); 0.02	6.02 (6.61); 1.39	7.51(7.97); 3.94***	407.60(559); 4.55***	152.00(187); 6.03***
IPL	0.10(0.10); 0.95	6.54(6.67); 2.57*	5.30(5.60); 0.37	5.94(6.27); 1.53	169.31(248); 4.31***	112.50(148); 5.26***
IFG	0.01(0.05); 0.22	1.06(1.06); 0.00	8.34(8.62); 9.21***	7.98(8.38); 6.49***	814.16(1160); 3.32***	311.17(399); 4.70***
pMTG	0.04(0.07); 0.51	5.47(6.01); 2.04†	7.11(8.25); 5.18***	1.01(1.01); 18.45***	446.03(618); 4.85***	262.84(348); 4.15***
<b>Gamma</b>						
ATL	0.02(0.04); 0.45	1.01(1.01); 0.00	8.52(8.95); 15.25***	8.44(8.93); 10.41***	62.84(558); 0.42***	165.71(186); 8.83***
IPL	0.04(0.03); 1.21	1.00(1.00); 0.00	7.17(8.36); 3.48***	8.33(8.90); 5.02***	23.98(248); 0.33***	112.34(148); 4.53***
IFG	-0.03(0.02); -1.72†	7.47(7.75); 13.46***	3.29(4.02); 0.21	3.19(3.89); 0.14	131.41(1159); 0.34***	326.64(400); 5.21***
pMTG	-0.01(0.03); -0.30	3.36(3.95); 0.54	6.05(7.03); 2.71**	4.61(5.46); 1.69	29.95(619); 0.15***	274.84(349); 4.69***

Note. Parameter estimates for each model (rows). The random effects are shaded in grey. edf, estimated degrees of freedom (values close to 1 indicate a linear relationship); rdf, reference degrees of freedom; fs, factor smooth; re, random effect (intercept); ATL, anterior temporal lobe; IPL, inferior parietal lobule; IFG, inferior frontal gyrus; pMTG, posterior middle temporal gyrus. Model specification: *bam(log(signal) ~ Trial\_Type + s(Time) + s(Time, by=Trial\_Type) + s(Time, Electrode, bs="fs") + s(subj\_word, bs="re")*). †*p* < .09, \**p* < .05, \*\**p* < .01, \*\*\**p* < .001.



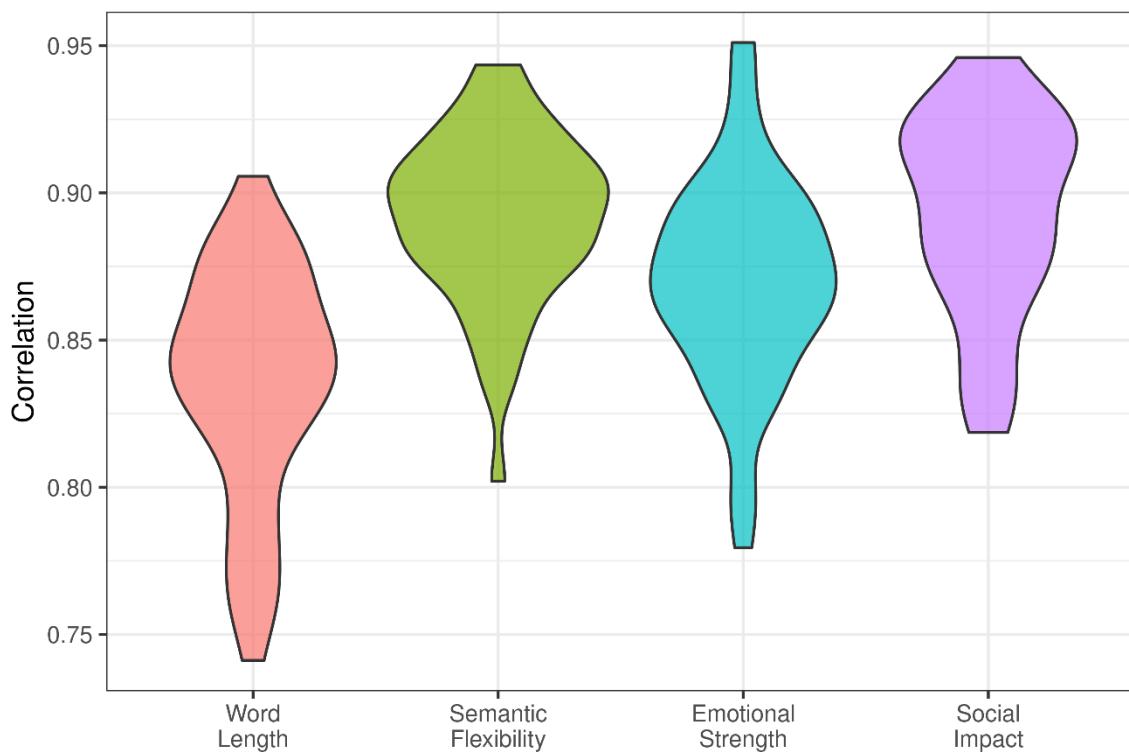


**Supplemental Figure 1. Model diagnostic plots.** The initial diagnostic plots (first 3 rows) indicated that the distribution of residuals was heavy tailed in the gamma models. To address this, these models were re-run using the scaled t family in the model specification. Those diagnostic plots are shown in the last row.

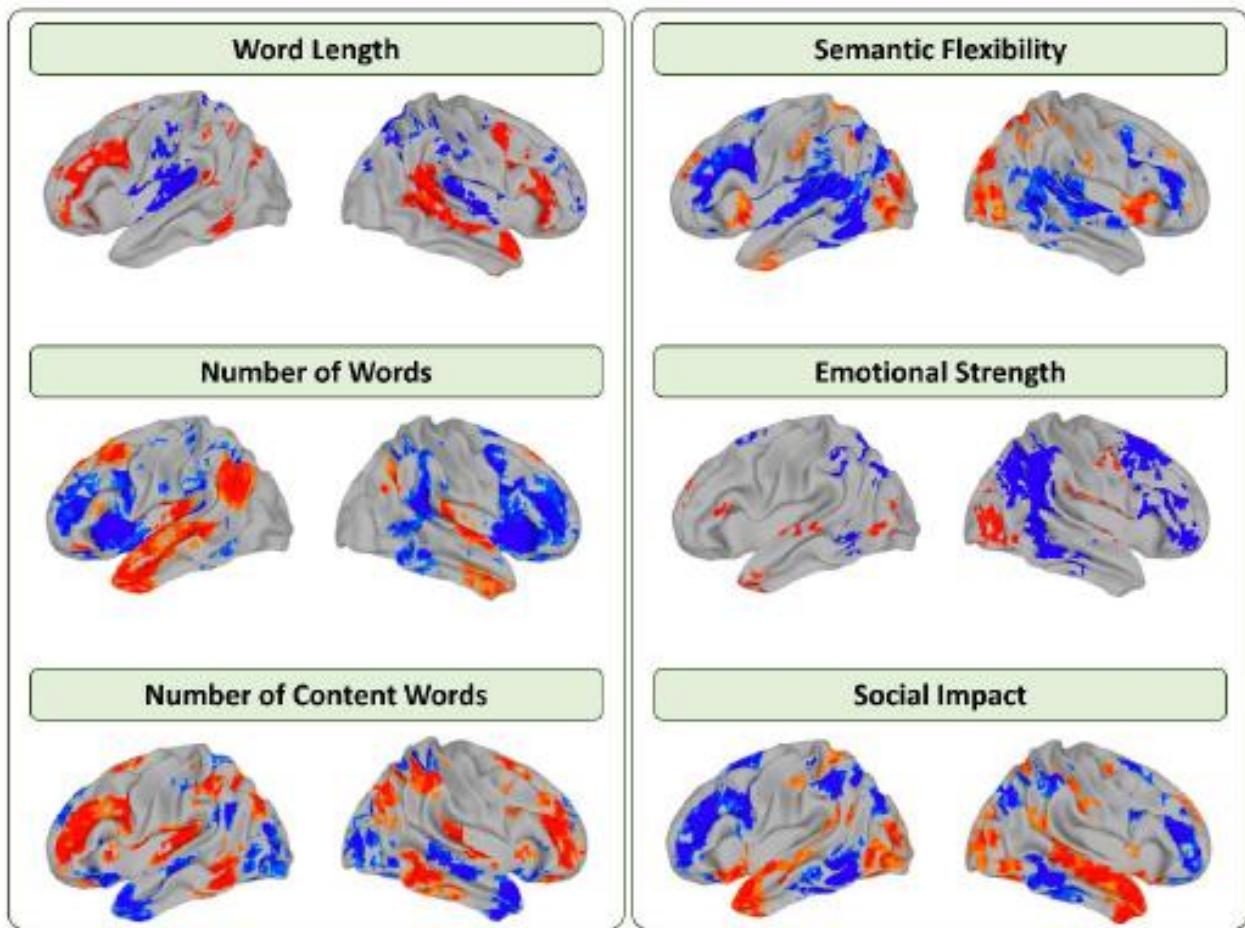


**Supplemental Figure 2. Time-frequency plots.** Frequency bands are indicated with dashed horizontal lines and the windows of significant condition differences within the theta and alpha band are indicated with vertical green or red lines. Taxonomic (top row), thematic (middle row), and the condition difference plot (bottom row) are presented for ATL, IPL, IFG, and pMTG separately. For the condition difference figures, red indicates greater power for taxonomic trials and blue indicates greater power for thematic trials.

## APPENDIX B: CHAPTER 3 SUPPLEMENTAL MATERIALS



**Supplemental Figure 1. Smoothed versus unsmoothed scores.** There was a high degree of correspondence between the smoothed vs unsmoothed factor score analyses at the subject-level ( $r = 0.74-0.95$ ). The subject-level correlations are visualized for each factor: (from right to left) Word Length (red), Semantic Flexibility (green), Emotional Strength (blue), Social Impact (purple).



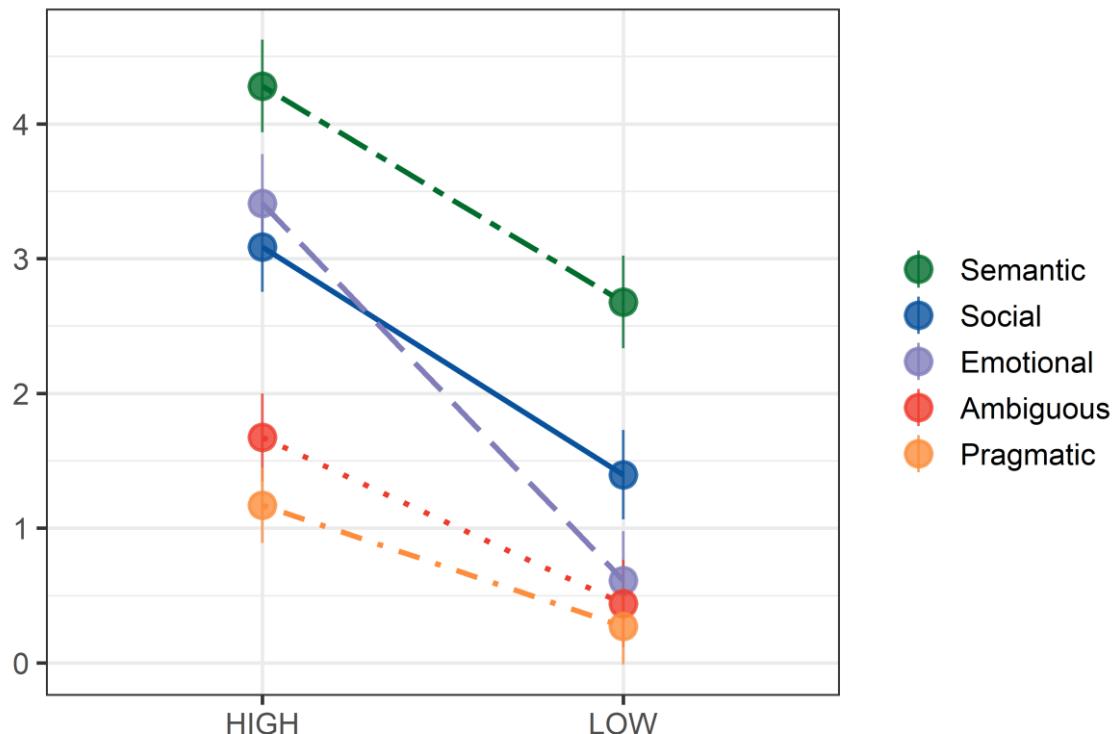
**Supplemental Figure 2. ClustSim Results.** The critical cluster size threshold was determined with Monte Carlo simulations implemented by AFNI's 3dClustSim program. These statistical maps are thresholded at a cluster-forming threshold of  $p < .01$  (91-108 voxels) and a family-wise error rate of  $p < .001$ . The results for the general lexical and semantic variables are shown in the left panel, and the results for the semantic concepts are shown in the right panel.

## **APPENDIX C: CHAPTER 4 SUPPLEMENTAL MATERIALS**

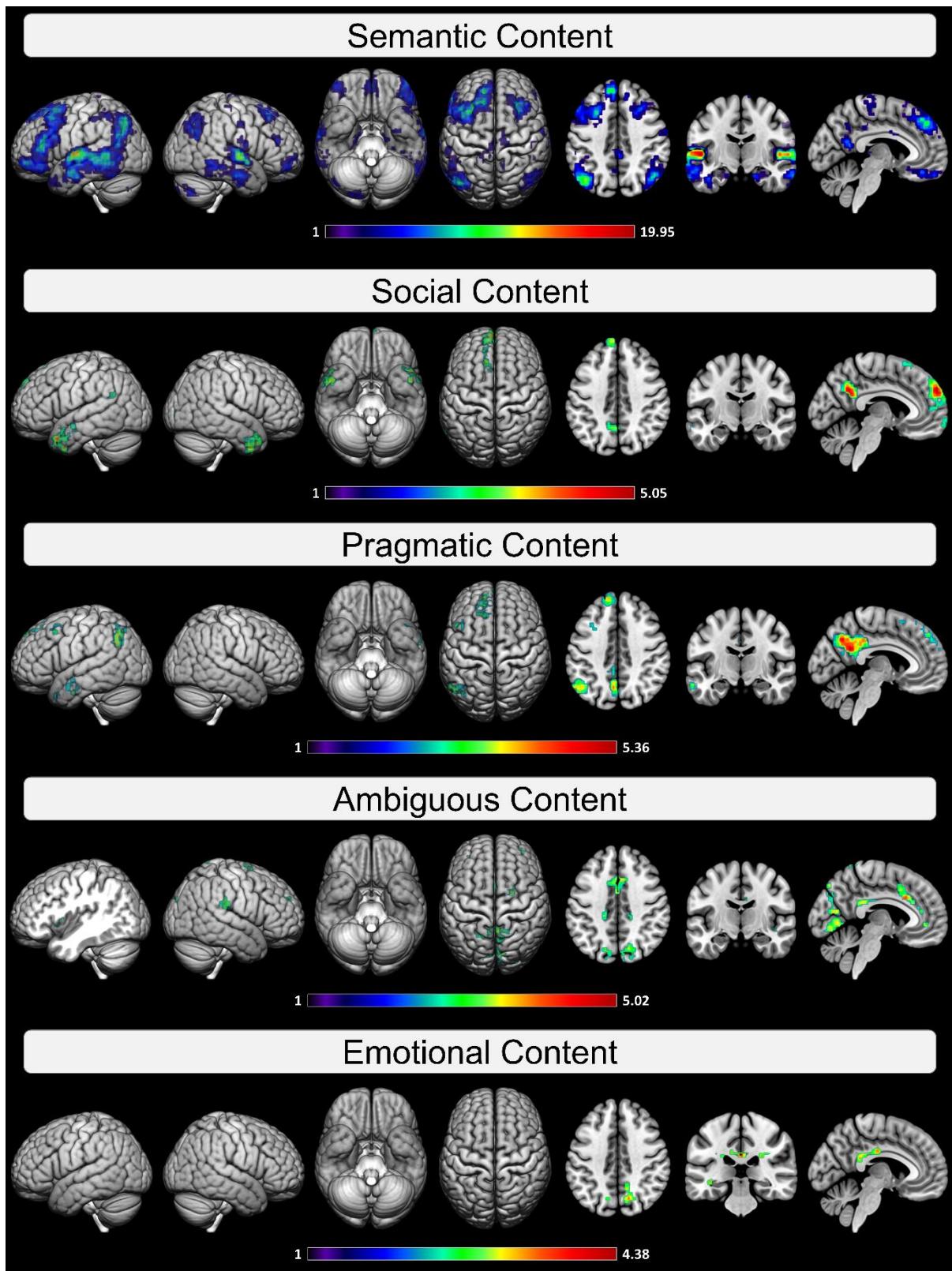
Sentence content coding was initially done using a numeric scale from 0 to 10 (as described in the Narrative Coding Protocol on OSF: <https://osf.io/mndvt>), with higher scores indicating more of a given content type. As the narrative coding progressed, it became apparent that the full range of ratings was not being used. As a result, two coding approaches were adopted in parallel. The first, numeric approach, was to continue applying the same, modified scale to ensure consistency in the application of ratings across the narrative. This is in contrast to emphasizing the use of more extreme scores partway through the narrative. The second, categorical approach, was to adopt a truncated, more readily separable scale by placing sentences in low, moderate, or high categories (used for analysis in the present study).

The numeric approach was done by 4 raters trained using the protocol and practice narratives. Regular meetings were held with the 4 raters to maintain consistent coding across the narrative and avoid any drift in how the coding was implemented. The categorical approach was done by the first author who developed the protocol and coded the practice narratives.

For the matched high and low sentences, correspondence between the two coding approaches was checked using a linear mixed effects model predicting the numeric ratings with a fixed effect of categorical rating and random effects of sentence and rater ( $n=4$ ). The correspondence between the numeric and categorical coding approaches was high: there was a significant categorical condition difference (i.e., high vs low) in the numeric ratings across all content types (see figure below).



**Supplemental Figure 1. Correspondence between categorical and numeric content coding approaches.** Regression coefficient estimates and standard error based on the numeric ratings for the matched sentences identified via categorical coding (i.e., HIGH and LOW).



**Supplemental Figure 2. Results thresholded using a more conservative threshold.** Thresholded Z-score statistical map showing lower (purple) to higher (red) values.

## APPENDIX D: CHAPTER 5 SUPPLEMENTAL MATERIALS

**Supplemental Table 1**

*Stage 1 Design Table*

Question	Hypothesis	Analysis Plan	Interpretation given to different outcomes
1. During naturalistic movie viewing, is semantic, social, and semantically flexible content associated with increased activation in the semantic, social, and semantic control networks, respectively?	1.1a (semantic words) Clusters of voxels showing increased activation in response to greater semantic word-level content will fall within the semantic brain network.	The word-level analyses will be the same for semantic, social, and semantically flexible content. The following steps will be taken for each measure independently:  (1) Extract smoothed time series of scores (either residual factor scores which account for number of words or number of content words) using a sliding window within event boundaries. (2) Whole-brain parametric modulation analysis. (3) The subject-level activation maps for a given content type will be used as inputs for a second-level group analysis using linear mixed-effects modelling with a fixed effect of content type and random intercepts of subject and movie.	Null: Fewer than 20 voxels will be associated with increased semantic information.  Alternatives: The clusters of voxels associated with increased semantic information will (1) include portions of the semantic network as well as regions outside the ALE-defined semantic network (partial support) or (2) fall entirely outside the ALE-defined semantic network (no support).
	1.1b (social words) Clusters of voxels showing increased activation in response to greater social word-level content will fall within the social brain network.		Null: Fewer than 20 voxels will be associated with increased social information.  Alternatives: The clusters of voxels associated with increased social information will (1) include portions of the social network as well as regions outside the ALE-defined social network (partial support) or (2) fall entirely outside the ALE-defined social network (no support).
	1.1c (control words) Clusters of voxels showing increased activation in response to semantically flexible		Null: Fewer than 20 voxels will be associated with increased semantically flexible content.  Alternatives: The clusters of voxels associated with increased semantic flexibility will (1) include

	word-level content will fall within the semantic control brain network.	(4) The statistical map will be corrected using a cluster-forming threshold of $p < 0.01$ and an FWE-corrected threshold of $p < 0.05$ (5) Results will be compared to the ALE-defined networks of interest, focusing on the core regions within each network, highlighted in the top panel of Figure 1.	portions of the semantic control network as well as regions outside the ALE-defined semantic control network (partial support) or (2) fall entirely outside the ALE-defined semantic control network (no support).
	1.2a (semantic events) Clusters of voxels showing increased activation in response to semantic events (plot-progressing, informative verbal or written scenes) will fall within the semantic brain network.	The event-level analyses will be the same for semantic, social, and scrambled content. The following steps will be taken for each measure independently:  (1) Whole-brain duration modulated parametric analysis. (2) The subject-level activation maps for a given content type will be used as inputs for a second-level group analysis using linear mixed-effects modelling with a fixed effect of content type and random intercepts of subject and movie. (3) The statistical map will be corrected using a cluster-forming threshold of $p < 0.01$ and an FWE-corrected threshold of $p < 0.05$	Null: Fewer than 20 voxels will be associated with semantic events.  Alternatives: The clusters of voxels associated with increased semantic information within events will (1) include portions of the semantic network as well as regions outside the ALE-defined semantic network (partial support), (2) fall entirely outside the ALE-defined semantic network (no support), or (3) produce the same clusters as the scrambled ratings (no support).
	1.2b (social events) Clusters of voxels showing increased activation in response to social events (scenes depicting on or off screen interactions between/among characters) will fall		Null: Fewer than 20 voxels will be associated with social events.  Alternatives: The clusters of voxels associated with increased social information within events will (1) include portions of the social network as well as regions outside the ALE-defined social network (partial support), (2) fall entirely outside the ALE-defined social network (no support), or

	within the social brain network.		(3) produce the same clusters as the scrambled ratings (no support).
2. To what extent are the semantic and semantic control networks involved in processing social concepts and events in individual subjects?	<p>2.1a (semantic overlap) If there are clusters of voxels that respond to social word and event-level content, then it is expected that both social concepts and social events will engage areas of overlap within the semantic brain network defined within individual participants.</p>	<p>The hypotheses of RQ2 will be tested using the following procedure:</p> <p>(1) The number of overlapping voxels will be calculated between the subject-level statistical maps for processing semantic and social content (word-level and event-level results processed independently)</p> <p>(2) The number of overlapping voxels will be calculated between the subject-level statistical maps for processing semantically flexible words and social content (word-level and event-level results processed independently).</p> <p>(3) A second-level random effects analysis will be run using the overlap images from individual participants to determine whether stable areas of overlap exist across participants.</p>	<p>Null: At the individual subject level, fewer than 10 voxels show increased activation in response to both semantic content and social content (either concepts or events).</p> <p>Alternatives: (1) clusters of voxels will show increased activation in response to semantic content and social concepts, but not social events (partial support) or (2) clusters of voxels will show increased activation in response to semantic content and social events, but not social concepts (partial support).</p>
	<p>2.1b (control overlap) If there are clusters of voxels that respond to social word and event-level content, then it is expected that both social concepts and social events will engage areas of overlap within the semantic control brain network defined within individual participants.</p>		<p>Null: At the individual subject level, fewer than 10 voxels show increased activation in response to both semantically flexible content and social content (either concepts or events).</p> <p>Alternatives: (1) clusters of voxels will show increased activation in response to semantically flexible content and social concepts, but not social events (partial support) or (2) clusters of voxels will show increased activation in response to semantically flexible and social events, but not social concepts (partial support).</p>
	2.2a (semantic non-overlap) If there are clusters of voxels that respond to social word		Null: At the individual subject level, the voxels which respond to social content will not be proximal to the voxels which respond to semantic content (i.e., the clusters of voxels will not be

	<p>and event-level content, then it is expected that non-overlapping, proximal clusters of voxels will differentially respond to semantic and social content.</p>	<p>subregions within a single atlas-defined anatomical region).</p> <p>Alternatives: (1) the voxels associated with processing social concepts, but not social events, will be proximal (i.e., subregions within a single anatomical region) to the voxels associated with processing semantic content (partial support) or (2) the voxels associated with processing social events, but not social concepts, will be proximal to the voxels associated with processing semantic content (partial support).</p>
	<p>2.2b (control non-overlap)</p> <p>If there are clusters of voxels that respond to social word and event-level content, it is expected that non-overlapping, proximal clusters of voxels will differentially respond to semantic control and social content.</p>	<p>Null: At the individual subject level, the voxels which respond to social content will not be proximal to the voxels which respond to semantically flexible content (i.e., the clusters of voxels will not be subregions within a single anatomical region).</p> <p>Alternatives: (1) the voxels associated with processing social concepts, but not social events, will be proximal (i.e., subregions within a single anatomical region) to the voxels associated with processing semantically flexible content (partial support) or (2) the voxels associated with processing social events, but not social concepts, will be proximal to the voxels associated with processing semantically flexible content (partial support).</p>

*Note.* The sampling plan is the same for all tested predictions. A sensitivity power analysis was conducted using the *pwr* package in R. With the fixed sample size of 86, statistical power of .95, and an alpha of 0.05, an omnibus multiple regression analysis with 2 to 3 predictors would be sensitive to detecting medium effects ( $\eta^2 = 0.19-0.21$ ).

<i>Category</i>	<i>Description</i>	<i>Rating</i>
<b>No Semantic Content</b>	<ul style="list-style-type: none"> <li>• No semantic content within the scene.</li> <li>• None of the characters share information with the audience via speaking, reading, or writing.</li> <li>• No information in the form of a narrative (either written or spoken) is provided.</li> </ul>	<b>1-2</b>
<b>Minimal Semantic Content</b>	<ul style="list-style-type: none"> <li>• Some semantic content within the scene.</li> <li>• Scene includes brief and/or limited semantic content such as a character (alone or with others) telling a short story or explaining a concept.</li> <li>• The primary purpose of the scene is not to convey semantic information.</li> <li>• Any semantic content that is shared might not be “new” to the viewer.</li> </ul>	<b>3-5</b>
<b>Moderate Semantic Content</b>	<ul style="list-style-type: none"> <li>• Much of the scene contains semantic content.</li> <li>• A character or narrator is providing a written or verbal narrative for the audience or the other characters in the scene. At least one primary purpose of the scene is to provide narrative exposition.</li> <li>• The amount, length, or novelty of the narrative information within the scene can be used to rate the relative degree of semantic content.</li> </ul>	<b>6-8</b>
<b>High Semantic Content</b>	<ul style="list-style-type: none"> <li>• The semantic content within the scene is present throughout the entire scene and is “new” information for the viewer.</li> <li>• In addition to the criteria outlined above for moderate semantic content, the primary purpose of the scene is to convey narrative or semantic information.</li> <li>• Almost none of the scene is non-semantic in nature.</li> </ul>	<b>9-10</b>

**Supplementary Figure 1. Rubric for how semantic content was rated for each minor event.** The rubric defines four broad categories (right) that are described (middle) and associated with a range of possible ratings to assign to a given event (left).

<i>Category</i>	<i>Description</i>	<i>Rating</i>
<b>No Social Content</b>	<ul style="list-style-type: none"> <li>• No social content is present within the scene.</li> <li>• Social stimuli (i.e., faces) may be presented briefly in scene, but not referred to.</li> <li>• There are no interpersonal interactions or conversations.</li> </ul>	<b>1-2</b>
<b>Minimal Social Content</b>	<ul style="list-style-type: none"> <li>• Some social content is present within the scene.</li> <li>• Scene includes brief and/or limited social content (i.e., short verbal or non-verbal exchange between characters such as waving at another character).</li> <li>• The primary purpose of the scene is not to convey social information.</li> <li>• Characters may have one-sided socially relevant monologues but do not engage in meaningful or lengthy conversations with other characters.</li> </ul>	<b>3-5</b>
<b>Moderate Social Content</b>	<ul style="list-style-type: none"> <li>• Much of the scene contains social content.</li> <li>• At least two characters are meaningfully interacting via verbal or non-verbal communication. This may occur in-person or over the phone. At least one primary purpose of the scene is to show characters interacting.</li> <li>• The salience or impact of the social information within the scene can be used to rate the relative degree of social content.</li> </ul>	<b>6-8</b>
<b>High Social Content</b>	<ul style="list-style-type: none"> <li>• The social content within the scene is present throughout the entire scene.</li> <li>• In addition to the criteria outlined above for moderate social content, the primary purpose of the scene is to convey social information or depict social interactions.</li> <li>• Almost none of the scene is non-social in nature.</li> </ul>	<b>9-10</b>

**Supplementary Figure 2. Rubric for how social content were rated for each minor event.** The rubric defines four broad categories (right) that are described (middle) and associated with a range of possible ratings to assign to a given event (left).