

**Behavioural and Neural Mechanisms for Sustaining Focus
during Semantic Cognition**

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Abstract

Semantic cognition enables both the comprehension of external information and the generation of internally oriented thought through flexible coupling and decoupling from perceptual input. This thesis investigated the cognitive and neural mechanisms underlying the maintenance of task focus supported by semantic cognition, focusing on how memory representations, control processes and perceptual information interact to sustain attention. Chapter 2 examined the neural basis of task focus across different cognitive processes. Sustained focus in comprehension and autobiographical memory recall was accompanied by the engagement of relevant memory systems and a disengagement of control networks, whereas focussed arithmetic was associated with reduced engagement of memory systems. Sustained comprehension showed mutual decoupling between control and memory networks. Chapter 3 investigated the content of ongoing thought and its relationship with task focus and performance. Task-unrelated thought involving future problem solving was more prevalent during difficult reading and associated with poorer comprehension, particularly for expository texts, whereas deliberate detailed thought was linked to higher focus and better comprehension, especially during narrative story reading. Overall, the alignment between ongoing thought and the demands of the semantic task was found to be critical for maintaining attention and influencing reading outcomes. Chapter 4 examined individual differences in intrinsic retinotopic coding, given the importance of perceptual coupling and decoupling for sustaining different types of thought. This chapter showed that patterns of retinotopic organisation modulate the relationship between neural activity and task focus in comprehension and autobiographical memory. Together, these findings suggest that sustaining focus during semantic cognition is associated with the continuous engagement of task-relevant memory representations both neurally and behaviourally. While cognitive neuroscience rarely examines the content of ongoing thought, this is shaped by task demands and associated with comprehension outcomes, while perceptual coding patterns further alter the balance of engagement of semantic, memory and executive control systems.

Table of Contents

Abstract.....	2
Table of Contents	3
List of Tables.....	7
List of Figures.....	8
Acknowledgements	10
Author's Declaration	11
Chapter 1. Introduction.....	12
1.1. Semantic cognition	13
1.1.1. Neural basis of semantic cognition	13
1.1.2. Semantic memory and episodic memory	17
1.1.3. Perceptual coupling and decoupling	19
1.2. Default mode network	22
1.2.1. Subsystems within DMN	22
1.2.2. Interaction with other networks	24
1.3. Thought patterns	27
1.4. Task attention.....	30
1.4.1. Executive control of task attention	31
1.4.2. Semantic processing and the DMN.....	33
1.5. Retinotopic coding during internal and external cognitive states	35
1.6. Aims and outlines of the thesis	38
Chapter 2. Distinct neural architectures of focus: Memory-related engagement is associated with control disengagement	42
2.1. Abstract.....	43

2.2. Introduction	43
2.3. Materials and Methods	46
2.3.1. Participants.....	46
2.3.2. Task Design and procedure.....	47
2.3.3. Materials.	48
2.3.4. fMRI data acquisition.	50
2.3.5. Multi-echo data pre-processing.....	50
2.3.6. fMRI data analysis.....	51
2.4. Results	52
2.4.1. Study 1: Differential focus effects during semantic and non-semantic tasks.....	52
2.4.2. Study 2: Effects of focus in comprehension versus autobiographical memory recall	57
2.4.3. Conjunctions of focus effects across Study 1 and Study 2	60
2.4.4. Effects of focus on functional connectivity	63
2.5. Discussion.....	64
Chapter 3. Mind-wandering content, not just frequency, predicts comprehension in narrative and factual reading	69
3.1. Abstract.....	70
3.2. Introduction	70
3.3. Methods	73
3.3.1. Participants.....	73
3.3.2. Task design and materials	73
3.3.3. Procedure	76
3.3.4. Analysis.....	76
3.4. Results	78

3.4.1. Effect of difficulty on mind-wandering	78
3.4.2. PCA results: Patterns of ongoing thought	78
3.4.3. Thoughts differences by difficulty and by text type	80
3.4.4. Thought patterns and comprehension accuracy	81
3.5. Discussion.....	82
Chapter 4. Retinotopic coding predicts individual differences in sustained focus during comprehension and recall	88
4.1. Abstract.....	89
4.2. Introduction	89
4.3. Methods	91
4.3.1. Participants.....	91
4.3.2. Task materials and procedures	92
4.3.3. fMRI data acquisition	95
4.3.4. fMRI data analysis	95
4.4. Results	99
4.4.1. Whole-brain distribution of positive and negative pRFs	99
4.4.2. Network analyses.....	101
4.4.3. PCA analysis results.....	103
4.4.4. Neural correlation of PCA components	104
4.5. Discussion.....	110
Chapter 5. Discussion	114
5.1. Introduction	114
5.2. Summary of each chapter	116
5.2.1. Chapter 2.....	116

5.2.2. Chapter 3.....	118
5.2.3. Chapter 4.....	119
5.3. Discussion.....	121
5.3.1. Sustaining Focus during comprehension and memory retrieval	121
5.3.2. The Role of the DMN in Perceptually Coupled and Decoupled Cognition.....	126
5.3.3. The Engagement of the Multiple-Demand Network in Sustained Cognition	128
5.4. Limitations and directions for future research.....	130
5.5. Conclusion.....	134
Appendices.....	135
Supplementary Information for Chapter 2.....	135
Supplementary Information for Chapter 3.....	147
Supplementary Information for Chapter 4.....	155
References.....	164

List of Tables

Table 3.1 MDES questions.....	75
Table 3.2 Results of generalized linear mixed model predicting comprehension accuracy from thought components for all texts.	82
Appendices	
Table S2.1 Study 1 linguistic properties of sentences, mean (SD).....	146
Table S2.2 Study 2 linguistic properties of cue words and sentences, mean (SD).....	146
Table S3.1 Results of generalized linear mixed model predicting comprehension accuracy from thought components for factual text.	152
Table S3.2 Results of generalized linear mixed model predicting comprehension accuracy from thought components for story text.....	152
Table S3.3 Results of generalized linear mixed model predicting mind-wandering frequency from reading time.	153
Table S3.4 Results of generalized linear mixed model predicting comprehension accuracy from reading time.....	153
Table S3.5 Results of linear mixed model predicting reading time from thought components for all texts.	153
Table S3.6 Results of linear mixed model predicting task focus from thought components for all texts.	154
Table S4.1. Summary of the linear mixed-effects model for the pRFs R^2 across network, hemisphere and pRFs.	160
Table S4.2 Pairwise comparisons of +pRFs vs. -pRFs within each network (Bonferroni-corrected).....	160
Table S4.3 ANOVA results for pRFs R^2 comparing adjacent networks by pRFs (Network $\times$ pRFs interaction).	161
Table S4.4 Summary of linear mixed-effects model results for pRF R^2 across subnetworks, hemisphere, and pRF type, for each functional network.	162

List of Figures

Figure 2.1 Task illustration and task focus ratings in two studies.	47
Figure 2.2 Parametric effects of task focus in Study 1.	54
Figure 2.3 Parametric effects of task focus in Study 2.	59
Figure 2.4 Conjunctions and task based functional connectivity.	61
Figure 3.1 Mind wandering differences across text difficulty and text type.	78
Figure 3.2 Patterns of ongoing thoughts differ by difficulty or text type.	79
Figure 4.1 Task paradigm.	93
Figure 4.2 Positive and negative pRFs throughout the cortex.	100
Figure 4.3 PCA loadings for the first three principal components identified in our analysis.	103
Figure 4.4 Relationship between PCA component 3 (default/limbic +pRFs) and focus-related brain activation.	105
Figure 4.5 Relationship between PCA component 2 (control/attention +pRFs) and focus-related brain activation.	107
Figure 4.6 Relationship between PCA component 1 (heteromodal -pRFs) and focus-related brain activation.	109

Appendices

Figure S2.1 Univariate activation results for comprehension and arithmetic in study 1 (N = 34).	140
Figure S2.2 Parametric effects of task focus for easy and hard comprehension and arithmetic in study 1.	140
Figure S2.3 Network analysis of focus effects in Study 1 and 2.	141
Figure S2.4 Univariate activation results for comprehension and autobiographical memory retrieval in study 2 (N = 26).	142
Figure S2.5 Task-based functional connectivity.	143
Figure S2.6 Task-based functional connectivity seeding from Control/Salience/DAN regions (A).	144
Figure S2.7 Task-based functional connectivity seeding from Core/MT DMN regions (A).	145

Figure S3.1 PCA analysis results.....	150
Figure S3.2 Reading time differences across text difficulty and text type.	151
Figure S4.1 Statistical significance of correlations between positive/negative retinotopic coding maps and the principal gradient was assessed using the spin permutation test (5000 permutations).....	157
Figure S4.2 Positive and negative pRFs throughout the cortex.	157
Figure S4.3 Scree plot showing eigenvalues for each principal component.	158
Figure S4.4 Heatmap of PCA loadings for principal components 1-6 identified in our analysis.	159

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Author's Declaration

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for a degree or other qualification at this University or elsewhere. All sources are acknowledged as references.

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Chapter 1. Introduction

Semantic cognition supports different thoughts and behaviours: we make sense of information from the external world, comprehending what we read or listen to (Lambon Ralph et al., 2017; Spitsyna et al., 2006), yet we also generate thoughts and memories that are independent of the external environment (Smallwood & Schooler, 2015; Zhang et al., 2022; Zhang et al., 2019). When attention is directed to external stimuli, semantic processing can be aligned with relevant perceptual input, enabling tasks such as reading comprehension through coupling between semantic representation and external visual inputs (Gonzalez Alam et al., 2025; Patterson et al., 2007). In contrast, when mind wanders to internally oriented processing, semantic activity supports self-generated thoughts that are relatively independent of ongoing perceptual information (Smallwood, 2011; Zhang et al., 2022). Therefore, sustained focus during semantic cognition likely depends on dynamic interactions between memory systems, control processes and perceptual coupling.

In tasks that require sustained semantic processing, such as text reading, cognitive states often fluctuate, with thought content ranging from knowledge relevant to the current task to internally generated, task-unrelated ideas (Mulholland et al., 2023; Paul Seli et al., 2018). Individuals need to suppress off-task thoughts, particularly instances of mind-wandering, to realize successful comprehension. Consistent with classical accounts, top-down control has been proposed to play a key role in maintain task focus; failures of executive control (McVay & Kane, 2010) or the availability of sufficient executive resources (Smallwood & Schooler, 2006), have been linked to the occurrence of mind-wandering. However, previous work has focused on tasks driven by external sensory input, paying less attention to the role of coherent, content-based representations in sustaining focus during semantic cognition. This thesis addresses this gap by investigating whether memory representations can sustain focus independently of continuous executive regulation and by examining how memory systems, executive control, and perceptual coupling interact to support sustained focus.

This introduction reviews the cognitive and neural mechanisms that support semantic cognition and sustained attention, focusing on how large-scale networks, ongoing thought and perceptual processes contribute to internally and externally oriented cognition. First, we introduce the theoretical framework of semantic cognition, focusing on the interaction between semantic representation and semantic control, and how these systems interact with episodic memory to support the construction of meaningful internal representations. We also consider how semantic cognition supports both perceptually coupled and perceptually decoupled cognitive states. Second, we examine the role of the default mode network (DMN) and its subsystems, highlighting how interactions between the DMN and other large-scale brain networks such as executive control and attention networks contribute to the regulation of internally and externally oriented cognition. Third, we discuss the heterogeneity of ongoing thoughts, linking neural activity to variations in on-task and off-task states. Interactions between large-scale brain networks are thought to support the continuity of ongoing experience, thereby supporting task attention. Fourth, we review the involvement of executive control in task attention, and discuss how the stable and coherent representations support sustained task focus during semantic cognition. Finally, we turn to the role of sensory engagement in sustaining task focus. Visual spatial organization is preserved in high-level cortical regions, and appears to support the interaction between perception, memory and semantic processing.

1.1. Semantic cognition

1.1.1. Neural basis of semantic cognition

Semantic cognition refers to the ability to flexibly use our conceptual knowledge to support thoughts and behaviours. The controlled semantic cognition (CSC) framework suggests that semantic cognition includes two interactive components: semantic representation to store long-term semantic knowledge, and semantic control to flexibly retrieve information that suits the goals and the context (Jefferies, 2013; Lambon Ralph et al., 2017).

1.1.1.1. Semantic representation

Various theories have sought to understand how semantic information is represented in the brain. For example, some suggest that semantic representations are grounded in sensory and motor distributed modality-specific cortex (Martin, 2007; Pulvermuller, 2005), supported by neuroimaging findings that the activation of semantic knowledge overlaps with perceptual and motor systems (Goldberg et al., 2006; Hauk et al., 2004; Trumpp et al., 2013). Based on this evidence, researchers suggested that semantic representation could be accomplished by the direct interaction between distributed modality-specific cortex (Martin, 2007). However, this distributed-only view has been challenged by evidence from neuropsychological data, where modality-specific content can be disrupted by damage to modality-specific brain regions, while conceptual processing is not measurably affected (Mahon & Caramazza, 2005; Rosci et al., 2003).

Patterson et al. (2007) proposed the hub-and-spoke theory of semantic representation, in which concepts rely on interactions between sensorimotor and abstract modality-independent representations. Consistent with the ‘embodied’ and distributed-only theory, the theory proposes that multimodal verbal and non-verbal experiences provide the core ‘ingredients’ for constructing concepts and that these information sources are encoded in modality-specific cortices, which are distributed across the brain (i.e., the ‘spokes’; Binder et al., 2016; Martin, 2016). Moreover, the theory proposes a single transmodal hub situated bilaterally in the anterior temporal lobes (ATLs), to support knowledge across all modalities (such as words, objects, pictures, or sound) and conceptual domains (such as animals, tools, faces and scenes) (Jefferies, 2013; Lambon Ralph et al., 2017). This theory is supported by converging evidence from neuropsychological, neuroimaging, and transcranial magnetic stimulation (TMS) studies (Coutanche & Thompson-Schill, 2015; Pobric et al., 2010; Pobric et al., 2007). For example, the repetitive TMS to lateral ATL slows down domain general semantic processing, whereas TMS to "spoke" regions affects processing of specific categories (Pobric et al., 2010; Pobric et al., 2007). This shows that both hub and spokes are important for semantic representations.

Though the ATL is thought to be a cross-modal hub representing semantic knowledge, it also shows graded transitions from both dorsal and medial ATL towards vATL (Jefferies & Wang, 2021; Lambon Ralph et al., 2017). Recent findings suggest that the cross-modal hub is centred on the ventrolateral ATL, with function changing gradually along the ATL moving away from this heteromodal peak (Lambon Ralph et al., 2017). Consistent with what would be expected of a heteromodal peak, the vATL activates strongly in semantic tasks irrespective of input modality and conceptual category (Binney et al., 2010; Visser et al., 2012). Moving away from the vATL peak, more medial ATL regions, closer to vision, respond more strongly to picture-based materials and concrete concepts than to other types of material (Hoffman et al., 2015; Visser et al., 2012). While the anterior superior temporal sulcus and superior temporal gyrus respond more strongly to auditory stimuli, spoken words, and abstract concepts (Hoffman et al., 2015; Visser & Ralph, 2011). Consistent with this graded view, studies of functional and structural connectivity show that superior parts of ATL connect more to auditory/somatosensory regions, ventromedial ATL with visual brain areas, and anterolateral ATL exhibits greater connectivity with semantically-relevant parts of the default mode network, including inferior frontal gyrus and anterior cingulate cortex that are related to controlled semantic processing (Bajada et al., 2017; Jackson et al., 2018; Jackson et al., 2016; Pascual et al., 2015).

1.1.1.2. Semantic control network

To suit the immediate task or context, semantic cognition must emphasize relevant aspects of knowledge and suppress irrelevant information (Jefferies, 2013; Lambon Ralph et al., 2017). For example, some tasks might require access to subordinate meanings, while others may need to overcome semantic ambiguity (Badre et al., 2005; Wagner et al., 2001). Semantic control processes can facilitate this dynamic access to contextually-relevant semantic representations, to allow us to flexibly retrieve relevant aspects of knowledge from the semantic store (Yee & Thompson-Schill, 2016).

According to the CSC framework, semantic control is implemented within a large-scale distributed neural network, that interacts with the semantic representations (Jefferies, 2013; Jefferies & Ralph, 2006; Lambon Ralph et al., 2017). Results from a series of fMRI

studies manipulating semantic control suggest that semantic control commonly activates a left-lateralized network, including left inferior frontal gyrus (IFG), posterior middle temporal gyrus (pMTG), dorsal AG bordering intraparietal sulcus and pre-supplementary motor area (Bonner et al., 2013; Davey et al., 2016; Noonan et al., 2013; Seghier et al., 2010; Snyder et al., 2011; Teige et al., 2019). Convergent evidence comes from lesion studies (Martin & Cheng, 2006; Metzler, 2001). In semantic aphasia (SA), damage to left inferior frontal or temporoparietal cortex affects the ability of semantic control (Gardner et al., 2012; Jefferies & Ralph, 2006; Thompson et al., 2015). The application of inhibitory TMS to the IIFG, pMTG and/or IPS transiently disrupts semantic functioning (Davey et al., 2015; Hoffman et al., 2015; Jackson et al., 2015; Whitney et al., 2011), suggesting that these regions have a crucial role in semantic control. Furthermore, a recent meta-analysis of 925 peaks over 126 contrasts delineated a multimodal and mostly left-lateralised semantic control network, consisting of inferior frontal gyrus, posterior middle temporal gyrus, posterior inferior temporal gyrus and -pre-supplementary motor area (Jackson, 2021; Noonan et al., 2013). These studies from lesion, fMRI and TMS provide convergent evidence to support the proposal that semantic control is a left-lateralized distributed network, situated in the context of the wider semantic network.

The distributed semantic control network is thought to be heterogeneous, drawing together regions that contribute to more domain-general executive control and that are more specific for semantic control (Alam et al., 2018; Dixon et al., 2018; Evgeniia et al., 2020; Jefferies, 2013; Whitney et al., 2011). General executive control is supported by regions in the frontal and parietal cortex (Duncan, 2010; Fedorenko et al., 2013), and brain activation in more dorsal and posterior aspects of the inferior frontal sulcus correlate with executive demands across multiple domains (Duncan, 2010). In contrast, regions such as anterior IFG and pMTG appear to be specific to semantic control, particularly when retrieval is effortful (Humphreys & Ralph, 2017; Jefferies, 2013). Studies of functional and anatomical connectivity have shown that the ventral IFG and pMTG are connected to ATL, whereas superior IFG shows no such connectivity (Davey et al., 2016; Humphreys & Ralph, 2017; Jackson et al., 2016). Taken together, these results suggest a gradation of the semantic control

network, in which more inferior regions are connected to the network for semantic representation to support retrieval of weakly encoded information, and more superior regions contribute to more domain-general control (Chiou et al., 2018; Chiou et al., 2023; X. Wang et al., 2020).

In summary, the sustained representation of semantic information is critical for maintaining coherent text comprehension. Regions such as ATL support the continuous extraction and integration of semantic content, providing meaningful representations that enable the interpretation of incoming information. At the same time, semantic control regions modulate this process by selecting and retrieving contextually appropriate meanings based on the current textual context. Together, the engagement of these distinct components of semantic cognition may help maintain cognition in a task-relevant state, thereby reducing the likelihood of mind-wandering. Ensuring the continuous representation of semantic information and its consistent alignment with the current contextual background may be an important mechanism for sustaining attention in reading.

1.1.2. Semantic memory and episodic memory

Semantic and episodic memory systems both contribute to the construction and maintenance of internal representations, which may help sustain focus during internally oriented tasks. Semantic cognition is typically associated with the retrieval and control of conceptual knowledge. However, internally oriented cognition, including the recollection of past experiences, often relies on the interactions between semantic and episodic memory systems. Although these two forms of memory were traditionally viewed as distinct (Tulving, 1972, 2002), much evidence suggests that they interact to support the representation of past experience and the construction of internally generated thoughts (Binder & Desai, 2011; Irish & Piguet, 2013; Renoult et al., 2019).

Tulving (1972) was the first to formally describe the distinction between episodic and semantic memory. Episodic memory refers to recollection of personally experienced events situated within a specific spatial-temporal context (Tulving, 2002). While semantic memory involves more with conceptual knowledge and is typically retrieved independently from the original spatial or temporal context. Evidence from neuropsychological studies provide some

support for the distinction between episodic and semantic memory. For example, patients with damage to the medial temporal lobes, have severe episodic memory impairments, with largely intact conceptual knowledge (Dickerson & Eichenbaum, 2010). In contrast, patients with semantic dementia have severe semantic impairments, but with relatively unimpaired episodic memory for new experiences (Patterson et al., 2007). Neuroimaging evidence also reveals that in contrast to the semantic cognition network, the episodic memory retrieval is associated with an extensive posterior medial network that mainly covers the retrosplenial, posterior cingulate cortices, angular gyri and the medial temporal lobe structures (Ranganath & Ritchey, 2012).

Nevertheless, several existing studies, both neuropsychological and neuroimaging, provided empirical evidence against a strict fractionation between episodic and semantic memory (Irish, 2020; Kim, 2016; Tibon et al., 2026). For example, patients with semantic dementia demonstrate that semantic knowledge is critical for the construction of novel future events, providing the necessary framework into which episodic information can be integrated (Irish et al., 2012). Neural evidence also reveals that the core episodic recollection network overlaps extensively with the semantic network, including in medial temporal lobes, middle temporal gyrus, ventral parietal cortex, and midline frontal and posterior cingulate cortex (for a review, see Renoult et al., 2019). Therefore, it is likely that semantic memory and episodic memory overlap and interact to support cognitive process. For example, a recent study identifies a shared region in the left inferior frontal gyrus extending towards the anterior insular cortex, which shows greater activity for controlled retrieval of both semantic and episodic memory (Vatansever et al., 2021). Semantic knowledge can provide a conceptual framework that organizes and constrains internally generated representations. By adopting a gradient perspective, a recent study proposed a concrete to abstract representation spectrum along modality-specific and default mode brain networks which collectively support rich and detailed memories (Irish & Vatansever, 2020). They argued that despite qualitative differences, both memory systems are anchored on the default mode network (DMN). These studies illustrate that, although there are differences in representation and retrieval between the two memory systems, the boundaries between the semantic and episodic memory are

blurred. These two systems overlap and interact, working together to support sophisticated cognitive processes.

In summary, semantic cognition plays an important role in constructing internal thoughts. Large scale networks such as DMN engaged during cognitive states that demand meaningful processing, providing semantic knowledge that helps to structure internally oriented content. By integrating semantic knowledge and memory representation, these networks support the generation of internally directed cognition. This raises the possibility of a competitive dynamic between externally oriented semantic processing, such as during reading, and internally generated thought. When the focus of attention fluctuates across different cognitive states, semantic resources may be dynamically reallocated. For example, under conditions of comprehension failure due to challenging text, semantic resources might be reallocated towards the generation of internal thoughts. However, the neural mechanism underlying such dynamic reallocation remain to be further explored.

1.1.3. Perceptual coupling and decoupling

As discussed above, semantic cognition supports not only externally oriented semantic processing, but also internally directed memory retrieval and spontaneous thought. These distinct cognitive states involve dynamic interactions between semantic representations and perceptual input, reflecting both coupling and decoupling of semantic cognition with perception (Fernandino & Binder, 2024; Shao et al., 2024; Zhang et al., 2022). Most recent study found different regions within default mode network (DMN) support perceptual coupled and decoupled during mind-wandering and reading, with left temporal and lateral prefrontal regions of DMN more activated during reading, while medial regions of DMN more recruited during memory retrieval (Zhang et al., 2022). In addition, evidence suggested that the MTG within DMN can underpin both off-task thought (e.g., autobiographical memory recall), and reading comprehension (Mattheiss et al., 2018; Zhang et al., 2022; Zhang et al., 2019), further highlighting the flexible engagement of semantic regions across perceptual coupling states.

1.1.3.1. Perceptually-coupled semantic retrieval

We deploy our conceptual knowledge to make sense of sensory inputs (Lambon Ralph et al., 2017; Patterson et al., 2007), such as comprehension of what we are reading or listening to (Friederici et al., 2000; Keidel et al., 2018; Spitsyna et al., 2006). Researchers have found that this perceptual-to-meaning processing involves different pathways in reading and listening comprehension (Saur et al., 2008). For visual processing, the ventral visual stream maps visual input onto conceptual representation, projecting from primary visual cortices to lateral and ventral occipital-temporal regions (James et al., 2003; Spitsyna et al., 2006). For auditory input, the ventral pathway of auditory pathways connects the middle temporal lobe and the ventrolateral prefrontal cortex via the extreme capsule, mapping sound-based representations of speech to widely distributed conceptual representations (Friederici, 2012; Saur et al., 2008). Several studies implicate the middle temporal lobe as a potential convergence area of visual and auditory ventral processing streams, crucial to capture the meaning during comprehension of what we perceive (Gauthier et al., 2012; Spitsyna et al., 2006).

It has also been observed that the regions within the lateral temporal lobe involved in conceptual processing, are tightly coupled with perceptual cortex (Chiou & Lambon Ralph, 2016, 2019; Clarke et al., 2013; Tyler et al., 2013; Zhang et al., 2019). Furthermore, a recent study found that individuals who remained focused on reading and who had better comprehension, had stronger intrinsic functional connectivity between primary visual cortex and a lateral temporal DMN region implicated in reading comprehension (Zhang et al., 2022). Taken together, these studies suggest that the lateral temporal regions within DMN form an important convergence zone for different kinds of input information and conceptual processing, interacting with both perceptually-coupled brain areas and regions of the DMN to make sense of the world (Deniz et al., 2019; Murphy et al., 2018; Zhang et al., 2022; Zhang et al., 2019).

1.1.3.2. Perceptually-decoupled semantic retrieval

While perceptual retrieval is often coupled to the external environment, it can also be perceptually decoupled during mind-wandering and/or autobiographical memory recall (Baird

et al., 2014; Pacheco Estefan et al., 2019; Simola et al., 2023; Smallwood et al., 2016). Mind-wandering is an experience in which attention drifts from the current task to self-generated thoughts and feelings (Smallwood & Schooler, 2006, 2015). Individuals who tend to be more off-task show greater decoupling between the DMN and regions of visual cortex important for visual processing during reading (Smallwood et al., 2013; Zhang et al., 2019).

Mind-wandering involves both the episodic memory system (Smallwood et al., 2013; Smallwood & Schooler, 2015) and semantic knowledge (Smallwood et al., 2016). It has been found that the tendency to mind wander associated with increased connectivity between the temporal pole and the hippocampal formation (O'Callaghan et al., 2015), which shows the importance of semantic knowledge in building the detailed content that characterises spontaneous thought (Smallwood et al., 2016). Besides, semantic knowledge and episodic memory interact, as evidenced by functional neuroimaging and clinical studies (Irish & Piguet, 2013; Irish & Vatansever, 2020; Stampacchia et al., 2018). Furthermore, impaired episodic future thinking correlates with semantic memory deficits in SD (Irish et al., 2012). It has also been found that verbal episodic memory tasks more rely on conceptual knowledge, since these inputs include little perceptual information that can act as a basis for encoding into episodic memory (Graham et al., 2002). These findings suggest that semantic knowledge also contribute to perceptually decoupled mental states.

In summary, semantic cognition supports both perceptually coupled processing, enabling us to make sense of the external world, and perceptually decoupled processing, which directs attention toward internal thoughts or memories. By flexibly engaging in perceptual coupling and decoupling, semantic representations facilitate the dynamic cognition between externally and internally directed attention. For instance, the lateral temporal cortex (LTC) underpins different mental states through changes in its functional connectivity with sensory input regions and other memory-related brain areas (Zhang et al., 2022). This suggests that shared semantic representations enable the transition between cognitive states by modulating their coupling with perception. If this is the case, coupling between the lateral temporal cortex and perceptual regions may be observed across different modalities. Moreover, these neural patterns of coupling and decoupling may not be driven solely by task

demands, but also emerge from fluctuations in attention. For example, as attention shifts over time, the degree of perceptual engagement may vary accordingly (Vatansever et al., 2017).

1.2. Default mode network

All mental states mentioned above, including semantic retrieval, memory recall and mind-wandering, are linked to activity within the default mode network (Christoff et al., 2016; Menon, 2023; Smallwood, Turnbull, et al., 2021). Default mode network (DMN) was traditionally defined as a network of regions that consistently exhibit deactivation during a wide variety of goal-directed behaviour, when compared with baseline state of brain activity, such as rest (Raichle et al., 2001). This network includes bilateral and largely symmetrical brain areas, in the medial and lateral temporal cortex, medial prefrontal cortex, and medial and lateral parietal cortex, as revealed by studies of large-scale intrinsic brain organization (e.g., Fox et al., 2005; Yeo et al., 2011). Recently, studies investigating the topographic location of DMN regions have found that the DMN is located at the end of information processing streams that are necessary for relatively abstract tasks, furthest away from sensory and motor systems (for review, see Margulies et al., 2016; Smallwood, Bernhardt, et al., 2021). This topographic location allows the DMN to process transmodal information that is unrelated to immediate sensory input, which may explain why the DMN is able to support the integration of diverse features from multiple sensorimotor regions, such as during semantic memory or episodic memory retrieval (Smallwood, Bernhardt, et al., 2021). Recent findings have shown that the DMN not only contributes to internally oriented mental processes, such as mind-wandering (Andrews-Hanna, Reidler, Huang, et al., 2010; Christoff et al., 2016), but also engages in externally-focused tasks, such as reading comprehension (Smallwood et al., 2013), semantic decisions (Krieger-Redwood et al., 2016), and demanding working memory tasks (Murphy et al., 2018; Vatansever et al., 2015).

1.2.1. Subsystems within DMN

It has been shown that DMN is composed of multiple distinct, yet interacting, subsystems with each subnetwork serving distinct cognitive functions (Andrews-Hanna, Reidler, Sepulcre, et al., 2010; Andrews-Hanna, Smallwood, et al., 2014; Yeo et al., 2011). Andrews-Hanna, Reidler, Sepulcre, et al. (2010) provided initial evidence for multiple

subsystems within DMN using hierarchical clustering analyses. They found the DMN is comprised of two distinct subsystems (corresponding to lateral temporal subsystem and medial temporal subsystem) that converge on a midline core (posterior cingulate and anterior medial prefrontal cortex). Yeo et al. (2011) replicated this finding by using whole-brain clustering approaches, showing stronger functional connectivity within subsystems than between subsystems. Both of these methodologies revealed three separable DMN ‘subsystems’ that serve distinct cognitive functions based on the brain regions within it.

One subsystem known as the dorsal medial subsystem, consists of the lateral temporal cortex, the temporal pole, dorsal medial prefrontal cortex and the temporoparietal junction. It has been shown to be important for semantic cognition (Jung & Ralph, 2023; Lambon Ralph et al., 2017; Wirth et al., 2011), particularly the lateral temporal cortex and left inferior frontal gyrus within this subsystem, which are implicated in the representation and retrieval of conceptual knowledge (Jackson et al., 2016; Jefferies, 2013; Lambon Ralph et al., 2017; Noonan et al., 2013). The ATL within lateral temporal cortex acts as domain general semantic hub supporting the integration of multiple sources of modality-specific information, into abstract conceptual representations (Lambon Ralph et al., 2017; Patterson et al., 2007). Another site in the anterior left inferior frontal gyrus plays an important role in controlled semantic retrieval (Badre & Wagner, 2007; Chiou et al., 2018; Noonan et al., 2013; Whitney et al., 2012). In addition, the dorsal medial subsystem also contributes to social and/or self-reflective aspects of autobiographical memory or future thought (Andrews-Hanna, Saxe, et al., 2014; Spreng & Grady, 2010).

The second subsystem comprised of hippocampus, parahippocampal cortex, retrosplenial cortex, the posterior inferior parietal lobe, and the ventromedial prefrontal cortex, is often referred to as the medial temporal subsystem. The medial temporal subsystem is reliably activated when individuals engage in autobiographical memory and episodic future thought (Andrews-Hanna, 2012; Buckner et al., 2008; Schacter et al., 2007), and individual’s increased resting-state functional connectivity within the medial temporal subsystem relate to the higher percentage of self-reported spontaneous past and future thought experienced during the resting state (Andrews-Hanna, Reidler, Huang, et al., 2010). These findings suggest an

important role for brain regions within the medial temporal subsystem in autobiographical and episodic memory (Eichenbaum et al., 2012; Horner et al., 2015; Steinworth et al., 2005).

The third subsystem engaged along the cortical midline, including posterior cingulate cortex, medial prefrontal cortex, and angular gyrus, is known as the core subsystem. This subsystem sits at points where medial and lateral temporal subsystems are spatially interdigitated (Braga & Buckner, 2017; Yeo et al., 2011), and might integrate information based on different aspects of knowledge to form coherent patterns of cognition (Andrews-Hanna, Smallwood, et al., 2014; Lanzoni et al., 2020). It has been found that the spatial patterns in medial temporal and posterior midline regions are correlated when encoding and rehearsing the same video clip, and this strength of correlation can predict the amount of information subsequently recalled (Bird et al., 2015). Smallwood et al. (2016) found that the association between spontaneous thought and the connectivity of the lateral and medial aspects of the temporal lobe converge on the posterior cingulate cortex, which indicated that the posterior core of the DMN acts as a representational hub that integrates information represented in medial and lateral temporal lobe and this process is important in determining the content and form of spontaneous thought. Another critical core DMN region, the medial prefrontal cortex, was functionally coupled with other DMN regions during autobiographical memory recall, prospection, and theory of mind tasks (Spreng et al., 2009). Besides, through its widespread connectivity with the PCC, the dorsal medial and medial temporal subsystems, limbic, and autonomic structures (Andrews-Hanna, Reidler, Sepulcre, et al., 2010; Roy et al., 2012), the medial prefrontal cortex is well positioned to integrate salient external or internal information (perhaps relayed from the PCC) with one's current affective experience and prior conceptual or episodic knowledge (Andrews-Hanna, Smallwood, et al., 2014). Taken together, the core subsystem is strongly functionally coupled with the other two DMNs subsystems and acts as a critical core to allow information to be integrated across subsystems.

1.2.2. Interaction with other networks

The DMN is involved in aspects of memory (e.g., semantic and episodic memory; Andrews-Hanna, Smallwood, et al., 2014; Smallwood, Bernhardt, et al., 2021), as well as decoupled states, such as mind-wandering (Smallwood, 2011; Smallwood & Schooler, 2015).

These processes also engage regions beyond the DMN, such as the semantic control network, attention networks and executive control regions (Andrews-Hanna, Smallwood, et al., 2014; Jackson, 2021). The DMN has been found to exhibit dynamic interactions with these brain networks (Andrews-Hanna, Smallwood, et al., 2014; Smallwood, Bernhardt, et al., 2021).

The DMN is anticorrelated with the dorsal attention network (DAN) (Fox et al., 2005; Keller et al., 2013), consisting of the posterior prefrontal cortex, the inferior precentral sulcus, the superior occipital gyrus, the middle temporal motion complex, and the superior parietal lobule (Corbetta & Shulman, 2002; Fox et al., 2005; Yeo et al., 2011). This network has been implicated in externally directed attention tasks (Buschman & Kastner, 2015; Corbetta & Shulman, 2002; Ptak, 2012) and its engagement results in the suppression of the DMN (Toro et al., 2008). As mentioned earlier, when self-generated thoughts occur, the processing of perceptual information is reduced, known as perceptual decoupling (Smallwood, 2013; Smallwood et al., 2012). This phenomenon is consistent with the inverted pattern between DMN and DAN, which support competitive relationships between the internal attention that occurs during self-generated thought and attention to external stimuli.

However, the DMN also coupled with the frontoparietal control network (FPCN) to facilitate goal-directed cognition (Krieger-Redwood et al., 2016; Spreng et al., 2010). Regions of frontal and parietal cortex appear essential for the orchestration of goal-directed behaviour and problem solving (Cole et al., 2013; Niendam et al., 2012). Functional connectivity of posterior cingulate cortex in DMN with dorsolateral prefrontal cortex was increased when participants performed demanding semantic tasks, even as the posterior cingulate cortex deactivated (Krieger-Redwood et al., 2016). Task-related functional connectivity analyses from Spreng et al. (2010) indicated that the FPCN was coupled with the DMN during autobiographical planning and with the dorsal attention network during visuospatial planning. Gao et al. (2013) observed a similar pattern of large-scale network interactivity as participants alternated between a motor sequence task and watching a movie. Furthermore, Dixon et al. (2018) used graph theory and meta-analytic functional profiling found that the FPCN is composed of two separate subsystems: FPCN_A is connected to the DMN and is involved in

the regulation of introspective processes, whereas FPCN_B is connected to the DAN and is involved in the regulation of visuospatial perceptual attention.

The semantic control network discussed above in Section 1.1.1.2 partially overlaps with DMN as well as executive control regions (Chiou et al., 2023; Davey et al., 2016; Wang et al., 2021) and the DMN is implicated in aspects of semantic control (Shao et al., 2024; Wang et al., 2021). Multivariate analysis revealed that the DMN regions encode semantic goal information associated with task-relevant semantic demands, whereas nodes of the semantic control network exhibited stronger intrinsic connectivity with frontotemporal DMN (Shao et al., 2024; Wang et al., 2021). In this way, the semantic control network is positioned between the DMN and executive control, fusing both to retrieval conceptual information that suits the demanding contexts (Chiou et al., 2023).

Finally, the DMN shows important relationships with perceptual systems. Traditionally, the DMN has been characterized as a network that operates relatively independently from immediate sensory processing (Buckner et al., 2008; Raichle et al., 2001). Activity within DMN regions is often associated with internally oriented cognition, such as memory retrieval, mental simulation, and spontaneous thought, which rely on abstract and conceptual representations rather than direct sensory input (Buckner et al., 2008). This relative decoupling from perceptual systems may facilitate cognitive processing that requires the integration of conceptual knowledge and memory representations. However, growing evidence suggests that it can flexibly interact with perceptual regions depending on task demands and cognitive states (Gonzalez Alam et al., 2025; Smallwood, Bernhardt, et al., 2021). For instance, during externally oriented tasks that integrate perceptual with conceptual knowledge, DMN regions show increased functional connectivity with sensory cortices (Deniz et al., 2019; Murphy et al., 2018; Simony et al., 2016), whereas during internally oriented states, they become relatively decoupled from perceptual input systems (Smallwood, 2013; Zhang et al., 2022). Positioned at the apex of the cortical hierarchy, the DMN is well placed to flexibly switch between these interactions with perceptual systems (Jefferies & Smallwood, 2025; Margulies et al., 2016; Paquola et al., 2025; Zhang et al., 2026). In this

way, the DMN may support cognition by dynamically regulating its interactions with perceptual networks across different cognitive states.

In summary, different subsystems within the DMN support distinct forms of cognition. Variations in the engagement of these subsystems, together with their interactions with other large-scale networks such as the executive control network, may enable the brain to flexibly support distinct cognitive states. Moreover, because the DMN occupies a high position within the cortical hierarchy, it can dynamically regulate its coupling with perceptual systems, allowing cognition to shift between externally oriented processing and internally generated thought. As a result, the engagement patterns of DMN may be associated with different patterns of thought. Importantly, as attention fluctuates over time, the relative contribution of these DMN subsystems, and their interactions with other networks, may also vary, giving rise to diverse patterns of ongoing thoughts.

1.3. Thought patterns

All cognitive systems described above interact dynamically to support a wide range of ongoing thought patterns. Ongoing thoughts appear to be heterogeneous and multidimensional, varying along dimensions such as internal versus external focus, semantic versus episodic content, and goal-directed versus spontaneous cognition (Mulholland et al., 2023; Smallwood, Turnbull, et al., 2021). Within this framework, some thoughts occur off task and are typically decoupled from external stimuli and are often associated with performance errors or reduced task engagement (McVay & Kane, 2010; Smallwood et al., 2009; Smallwood & Schooler, 2015). In contrast, other thought patterns can align with current task goals, for example through retrieval of relevant prior knowledge, thereby supporting ongoing task performance (Seli et al., 2016; Spreng et al., 2010; Turnbull et al., 2020; Turnbull, Wang, Murphy, et al., 2019). The diversity of thought content reflects the variability of cognitive states and is associated with diverse patterns of neural activation across large-scale brain systems (Dixon et al., 2018; Karapanagiotidis et al., 2020).

Multidimensional experience sampling (MDES) was widely used to probe the dynamics of ongoing thoughts both in lab and in daily life (McKeown et al., 2023; Mulholland et al., 2023; Smallwood et al., 2016; Smallwood, Turnbull, et al., 2021). MDES

requires participants to describe the content of their ongoing experiences along multiple dimensions. For example, using a continuous scale from 1 (Not at all) to 10 (Completely), participants may report whether their thoughts involve future event whether they are emotionally positive or negative, and whether they are experienced as words or images. These data can then be decomposed to identify thought patterns that vary across multiple dimensions. MDES has been used to capture both on-task and off-task cognition (McKeown et al., 2023; Smallwood et al., 2016; Smallwood, Turnbull, et al., 2021; Turnbull, Wang, Murphy, et al., 2019). For example, MDES measures of sensory engagement have been linked to better memory for information across during movie watching, whereas off-task thought captured by MDES often involves personal future planning or autobiographical memory retrieval (Turnbull, Wang, Murphy, et al., 2019; Wallace et al., 2025). MDES is also sensitive to the brain activity changes reflected by fMRI. Studies combining MDES with neuroimaging have shown that variations in ongoing thought correspond to different configurations of large-scale brain networks, including the DMN and executive control networks (Ho et al., 2019; Karapanagiotidis et al., 2017; Karapanagiotidis et al., 2020; Konu et al., 2020; McKeown et al., 2020; Turnbull et al., 2020; Turnbull, Wang, Murphy, et al., 2019; Vatansever et al., 2020). Together, these findings demonstrate the utility of MDES in linking subjective experience to large-scale brain activity.

Converging evidence from neuroimaging studies suggests that distinct patterns of ongoing thoughts are systematically organised across large-scale brain networks (Christoff et al., 2016; Smallwood, Turnbull, et al., 2021; H.-T. Wang et al., 2020; Wang et al., 2017). In particular, activity within DMN has been consistently linked to patterns of experience characterised by internally generated content, including autobiographical memory retrieval, future thinking, social cognition, and self-referential processing (Andrews-Hanna, Reidler, Huang, et al., 2010; Andrews-Hanna, Saxe, et al., 2014; Karapanagiotidis et al., 2017; Smallwood et al., 2016; Sormaz et al., 2018). In contrast, activity in FPCN has been associated with thought patterns characterised by sustained task focus, deliberate processing, and strong coupling between attention and the prioritisation of goal-relevant information (McKeown et al., 2023; Turnbull et al., 2020; Turnbull, Wang, Murphy, et al., 2019). These

patterns of experience often involve sustained attention to task-relevant stimuli and active maintenance of goal-relevant information. However, FPCN has also been implicated in the flexible, context-dependent regulation of ongoing thought. For example, Turnbull, Wang, Murphy, et al. (2019) showed that activity in dorsolateral prefrontal cortex, a core region of FPCN, was associated with increased on-task thought during a demanding working memory task, but also with greater off-task thought when task demands were reduced. In addition, activity in sensory cortex have been linked to experiential states characterised by greater sensory engagement and multimodal perceptual experience during naturalistic cognition such as movie watching (Wallace et al., 2025).

Evidence from functional connectivity and naturalistic paradigms suggests that ongoing thought appears to be associated with coordinated interactions between multiple large-scale brain systems (Karapanagiotidis et al., 2020; McKeown et al., 2020; Medea et al., 2018; Wang et al., 2018). For example, the capacity of an individual to generate off-task thought in a low-demand condition was associated with context-dependent prioritisation of internally generated cognition, accompanied by reduced coupling between neural systems supporting external task processing (including posterior DAN) and lateral DMN regions supporting internally generated cognition (Turnbull, Wang, Murphy, et al., 2019). Similarly, variations in detailed experience and representational format have been associated with coordinated activity across DMN, executive control, and sensory systems (Ho et al., 2019; Karapanagiotidis et al., 2020). Naturalistic neuroimaging work further demonstrates that complex real-world experience often requires coordinated recruitment of multiple large-scale systems supporting perceptual processing and conceptual integration (Simony et al., 2016). Importantly, the relationship between ongoing thought and large-scale brain networks appears to be dynamic, with thought patterns fluctuating alongside changes in global brain state (Christoff et al., 2016; Smallwood, Turnbull, et al., 2021). Consistent with this view, experience sampling studies indicate that fluctuations in ongoing thought are associated with transitions between distinct large-scale brain states, including changes in coupling between attention systems and networks supporting internally generated cognition (McKeown et al., 2023; Turnbull et al., 2020; Turnbull, Wang, Schooler, et al., 2019). Together, coordinated

activity across large-scale brain networks gives rise to the diverse forms of thought that characterise ongoing experience.

In summary, thought experience is highly heterogeneous, and fluctuations in thought experience reflect continuous changes in cognitive state. The evidence reviewed above suggests that dynamic coupling and reconfiguration across large-scale brain networks support different forms of thought content and underlie complex cognitive function. However, many brain networks, particularly executive control systems and memory-related networks, not only support internally generated thought but also contribute to stable task engagement when required. This dual role highlights the importance of these brain networks in balancing internally oriented cognition and externally directed task attention.

1.4. Task attention

As discussed above, thought patterns are highly heterogeneous across different cognitive states, yet maintaining consistency of thought content is essential for sustaining attention and supporting stable cognitive processes. Semantic cognitive tasks such as reading involve the continuous integration of information, which demands the ability to sustain attention on task-relevant content (Barbey et al., 2014; Jefferies, 2013; Lambon Ralph et al., 2017). Task attention plays a critical role in semantic cognition by enabling individuals to maintain coherent and sustained patterns of thought, ensuring that incoming information is interpreted in relation to ongoing goals and prior context (Lambon Ralph et al., 2017; Smallwood & Schooler, 2006, 2015; Smallwood, Turnbull, et al., 2021). Importantly, this process is not limited to the selection of relevant stimuli, but also involves the active maintenance and updating of task-relevant representations (Duncan, 2010; Engle & Kane, 2004). Consistent with this view, recent work has linked sustained attention to interactions among large-scale brain networks, including executive control systems and default mode network, highlighting the distributed and dynamic neural basis of task engagement (Fortenbaugh et al., 2017; Fortenbaugh et al., 2018; Rosenberg et al., 2020; Smallwood, Bernhardt, et al., 2021).

1.4.1. Executive control of task attention

Task attention is conventionally viewed as a product of top-down control relying on executive control mechanisms, which support stable cognitive performance by maintaining task goals and suppressing task-irrelevant interference (Diamond, 2013; Draheim et al., 2022; Duncan, 2010). From this perspective, executive control allocates cognitive resources to support goal-directed processing, and the failures in control can result in performance variability, distraction, and mind-wandering (McVay & Kane, 2012). Research on task difficulty in general cognitive paradigms has shown that mind-wandering varies as a function of task demands, with lower task difficulty typically associated with higher rates of mind-wandering (Forster & Lavie, 2009; McKiernan et al., 2006). The executive-resource hypothesis explains this finding as the competition of cognitive control (Smallwood & Schooler, 2006, 2015). When task demands are lower, fewer executive resources are required to support task performance, leaving the remaining executive capacity available to activate internally generated thoughts. In contrast, the control failure account proposes that mind-wandering arises when executive control mechanisms fail to maintain task goals in an active state, allowing task-unrelated thoughts to intrude into ongoing cognition (McVay & Kane, 2010). From this perspective, mind-wandering reflects a failure of the executive-control system to adequately combat interfering thoughts that are generated and maintained automatically, rather than being generated through the use of executive resources. Although these accounts differ in their proposed mechanisms, they converge in emphasizing the critical role of executive control in maintaining stable task engagement. Neuroimaging findings provide further support for this perspective. Using a sustained attention to response task (SART), Christoff et al. (2009) showed that mind-wandering was associated with increased activation in the medial prefrontal DMN, reflecting internally generated thought. Importantly, mind-wandering episodes were also accompanied by activation in executive network, indicating that executive resources may contribute to the generation and maintenance of internal thoughts (Smallwood & Schooler, 2006).

Converging evidence support that the executive control mechanisms play an important role in supporting stable task engagement under conditions of distraction,

uncertainty, and fluctuating cognitive demand (Fortenbaugh et al., 2017; Rosenberg et al., 2020). These processes involved in a large scale of networks that important for attention, including dorsal attention and ventral attention systems, salience network and the executive network (Caruana et al., 2015; Christoff et al., 2016; Fox et al., 2015; Hasenkamp et al., 2012). For example, the dorsal attention network, encompassing lateral parietal, occipital, and frontal regions, is consistently engaged during top-down attentional orienting and goal-directed selection of task-relevant sensory information, whereas the ventral attention network, including anterior insula, anterior cingulate cortex, temporoparietal junction, and ventrolateral prefrontal regions, supports the detection of behaviourally salient information and flexible reorientation of attention (Corbetta & Shulman, 2002; Turnbull, Wang, Schooler, et al., 2019; Vossel et al., 2014). Executive networks are most often engaged when participants focus on a task, to avoid mind-wandering, especially when the cognitive demand increases (Corbetta & Shulman, 2002; Fedorenko et al., 2013; Woolgar, Williams, et al., 2015), and these may reflect an increase in cognitive scaffolding to achieve the task goal (Duncan, 2010; Favila et al., 2018; Jackson et al., 2017; Woolgar, Afshar, et al., 2015; Woolgar et al., 2011). This engagement of control networks is seen even when the outcome is unsuccessful (e.g., inaccurate performance, increase in mind-wandering). For example, Esterman et al. (2014) found that more erratic, error prone performance (i.e., being out of the zone) was associated with greater engagement of control regions. Importantly, executive control systems may also support context-dependent prioritisation of internally generated thought when external task demands are reduced. For example, activity in the left dorsolateral prefrontal cortex has been linked to the prioritisation of off-task thought in low-demand contexts, suggesting that control processes may regulate the balance between externally and internally directed cognition rather than simply suppressing internally generated thought (Turnbull, Wang, Murphy, et al., 2019).

In addition, increasing evidence suggests that task attention emerges from dynamic interactions among multiple large-scale brain networks, rather than isolated engagement of executive control systems (Cole et al., 2013; Fox et al., 2015; Menon & Uddin, 2010). In particular, interactions between executive control networks and the DMN also play a critical role in regulating the balance between externally oriented task processing and internally

generated thoughts (Christoff et al., 2016; Spreng et al., 2010). For example, the FPCN has been shown to support flexible shifts in attention by dynamically altering its coupling with other large-scale systems, coupling with the DMN to support internally focused autobiographical planning, or with the dorsal attention network to support externally focused visuospatial processing (Dixon et al., 2018). Consistent with this, sustained attention has been linked to intrinsic fluctuations in large-scale network dynamics rather than a fixed attentional capacity (Rosenberg et al., 2020; Turnbull, Wang, Schooler, et al., 2019). Individual differences in attention stability appear to be shaped by the functional integration between control and default mode systems, highlighting the importance of network coordination in maintaining stable cognitive states (Turnbull, Wang, Schooler, et al., 2019). Overall, task attention is closely linked to executive control mechanisms, with stable task engagement supported both by the engagement of control processes and their dynamic interactions with internally oriented networks such as the DMN.

1.4.2. Semantic processing and the DMN

Beyond general attentional control, sustaining task attention often depends on the stability and ongoing construction of task-relevant internal representations. This is particularly evident in complex cognitive activities such as reading, which requires the continuous generation, integration, and updating of semantic representations over time (Lambon Ralph et al., 2017). In such contexts, sustaining attention involves not only suppressing distraction, but also maintaining coherent internal representations that support ongoing comprehension and reasoning (Smallwood, 2011; Smallwood & Schooler, 2015).

Reading comprehension is widely thought to depend on the construction of situation models that integrate semantic memory with episodic and contextual information to form coherent mental representations of text meaning (Andrews-Hanna, Reidler, Huang, et al., 2010; Smallwood, 2013). Importantly, internally generated cognition, such as mind-wandering or spontaneous thought, also relies on similar semantic and episodic memory systems to construct internally generated situation models (Smallwood et al., 2016; Smallwood, Turnbull, et al., 2021). Mind-wandering is typically interpreted as a failure of executive control (Kane & McVay, 2012; McVay & Kane, 2010) or the availability of

sufficient executive control resources (Smallwood & Schooler, 2006), with increasing mind-wandering in easy tasks. However, mind-wandering during reading is more complex. Although some research showed that easy reading tasks are associated with more mind-wandering, emerging studies of reading comprehension have repeatedly shown that mind-wandering occurs more frequently during the processing of more difficult texts (Feng et al., 2013; Kahmann et al., 2022; Soemer et al., 2019). One possible explanation is that externally oriented tasks such as reading and internally oriented cognition such as mind-wandering may compete for shared representational resources stored in long-term memory. Increased semantic processing demands increase the likelihood of failures in semantic mapping or integration, reducing the stability of internal task models and increasing susceptibility to task-unrelated thought. Evidence from semantic cognition research further suggests that semantic retrieval and integration processes are more error-prone or resource-demanding under conditions of increased semantic complexity (Jefferies, 2013; Lambon Ralph et al., 2017). Neuroimaging research further supports the role of internal representational systems in sustaining attention. The DMN has been increasingly implicated in semantic cognition, episodic memory, and internally generated simulation processes, all of which contribute to the construction and maintenance of internal situation models (Shapira-Lichter et al., 2013; Smallwood, Bernhardt, et al., 2021; Weiller et al., 2022). Variations in DMN engagement and connectivity may therefore influence the stability of internally generated task representations and, in turn, the stability of attention (Smallwood, Turnbull, et al., 2021; Turnbull, Wang, Murphy, et al., 2019). Finally, recent electrophysiological work suggests that sustained attention can involve functional decoupling from sensory input, reflecting increased reliance on internally generated representations during complex cognitive processing (Simola et al., 2023). Together, these findings suggest that sustaining task attention in complex semantic tasks may depend not only on executive control, but also on the successful generation and maintenance of internal representational models.

In summary, task attention does not rely solely on attentional and executive control networks, but also depends on brain systems that maintain internal representations of task-relevant information. In particular, the DMN may contribute to sustaining task engagement by

supporting the construction and maintenance of semantic and episodic representations that structure ongoing thought. This issue may be especially relevant for complex cognitive tasks such as reading comprehension, which rely heavily on the continuous integration of semantic and episodic information. However, the neural mechanisms underlying fluctuations in reading attention remain unclear. Given the strong reliance of these tasks on semantic and episodic representations, it is possible that task engagement may not depend exclusively on executive control processes. Instead, representational systems such as the DMN may play an important role in maintaining coherent task-related thought during sustained cognitive processing. The coupling between the DMN and perceptual systems may enhance task focus in semantic contexts (Zhang et al., 2022), whereas in some cases, a decoupled state may facilitate the retrieval of task-relevant knowledge (Murphy et al., 2018; Smallwood, 2013). Therefore, a full understanding of focus in semantic tasks needs to consider the integration of visual information into the DMN.

1.5. Retinotopic coding during internal and external cognitive states

Previous sections have highlighted the role of semantic cognition in supporting both perceptually coupled and perceptually decoupled cognitive states. As attention shifts between the external environment and internally generated thoughts, conceptual processing must interact with perceptual systems to maintain coherent cognition. This raises an important question: how are conceptual representations within semantic networks coordinated with sensory inputs when cognition transitions between internally and externally oriented states? One possible mechanism is the presence of shared spatial coding principles that allow perceptual and internally generated representations to interact within a common representational framework.

Traditionally, retinotopic coding, where neural responses are organized according to positions in the visual field, has been considered restricted to early visual cortex. In these regions, neighbouring neural populations correspond to neighbouring locations in visual space, forming well-known retinotopic maps that support the processing of visual input. Under this view, retinotopic coding is thought to be replaced by abstract amodal coding as information propagates from the visual hierarchy to the memory systems located at the apex

of the cerebral cortex (Groen et al., 2022; Margulies et al., 2016; Popham et al., 2021; Wandell et al., 2007). However, recent studies have challenged the idea that retinotopic organization is confined to early sensory cortices. Evidence from neuroimaging and population receptive field modelling suggests that retinotopic biases or spatial tuning can also be observed in higher-level visual areas beyond the early visual system (Klink et al., 2021; Knapen, 2021; Silson et al., 2016; Szinte & Knapen, 2020). For example, eccentricity bias has been proposed as an organizing principle for object-selective regions in ventral visual cortex (Hasson et al., 2002). Retinotopic structure has also been reported in scene-selective regions such as parahippocampal place area and occipital place area (Silson et al., 2015; Silson et al., 2021; Steel et al., 2021). These findings suggest that spatial coding based on visual field position continues to influence the organization of higher-level visual processing regions.

More recent studies have extended observation of spatially organized responses to visual field location beyond early visual cortex to large-scale cortical networks, including parietal cortex, lateral temporal cortex, and portions of frontal cortex (Knapen, 2021; Mackey et al., 2017; Szinte & Knapen, 2020). For example, retinotopic visual field maps have been identified in frontoparietal regions involved in visual attentional and cognitive control, suggesting that spatial coding based on visual coordinates extends into large-scale networks (Mackey et al., 2017). Consistent with this view, recent evidence indicates that retinotopic coding is also present in higher-order cognitive networks, including regions overlapping with DMN (Klink et al., 2021; Knapen, 2021; Silson et al., 2021; Szinte & Knapen, 2020). The spatial tuning properties of neural populations (i.e., population receptive field, pRF) have been widely used to map retinotopic organization in both low- and high-level visual areas. Using a pRF model capable of capturing both BOLD signal increases and decreases, Szinte and Knapen (2020) reported that DMN regions contain visually evoked pRFs with inverted response amplitudes. Specifically, they showed that deactivation signals in DMN regions could be predicted based on the spatial position of visual stimuli, suggesting that the default networks may function as a negatively modulated, high-level visual network. These findings challenge the traditional view that spatial visual coding is restricted to sensory cortices and

instead suggest that retinotopic organization may provide a broader computational scaffold across the cortex.

Recent research has begun to examine the relationship between retinotopic organization and memory systems. Studies investigating scene perception and scene memory have revealed a close spatial relationship between cortical regions involved in these processes. For example, research has identified a posterior–anterior distinction in medial parietal cortex, in which posterior regions are primarily involved in scene perception, whereas more anterior regions support scene memory and scene construction (Silson et al., 2019). Further evidence suggests that perceptual and mnemonic systems may be linked through spatially organized cortical networks. Studies examining the interaction between scene perception and spatial memory have identified cortical networks that connect perceptual regions with memory-related areas in posterior cortex (Steel et al., 2021). More recent research has used both positive and negative pRFs to reveal robust inverted (negative) retinotopic coding in category-selective memory areas at the cortical apex, which is functionally linked to the classic positive retinotopic coding in category-selective perceptual areas within high-level visual cortex (Steel et al., 2024). These findings suggest that retinotopic coding may play a crucial role in scaffolding communication between perception and memory systems. Moreover, Knapen (2021) used topographic connectivity analyses to demonstrate retinotopic processing in higher-level brain areas independent of specific task demands, revealing distinct connectivity patterns during movie watching and resting state. These results suggest that the visual role of DMN and hippocampus may allow these regions to interface between abstract memories and concrete sensory impressions. Taken together, these findings indicate that retinotopic coding based on visual coordinates may extend to high level systems involved in memory and internally generated cognition, potentially acting as a spatial scaffold that links perception and memory systems.

In summary, retinotopic coding extends beyond early visual cortex and can be observed across multiple levels of cortical organization. Early studies demonstrated retinotopic organization within occipital visual areas, while subsequent work revealed spatial coding in higher-level visual regions involved in object and scene processing. More recent

research has further shown that retinotopic coding is present in large-scale cortical networks, including frontoparietal regions and areas overlapping with the DMN. Importantly, emerging evidence indicates that spatially organized responses may also link perceptual and memory-related systems, with retinotopic coding observed in both perceptual regions and higher-level areas involved in scene memory and internally generated cognition. These findings suggest that retinotopic organization may act as a shared spatial framework, thereby helping to coordinate interactions between perceptual information and memory-based processes across the cortex. Within this framework, retinotopic coding in higher-order cortex may play a role in balancing externally driven attention, semantic processing, and internally generated cognition. However, it remains unclear how retinotopic coding supports semantic processing across different cognitive states, particularly when attention fluctuates within externally oriented cognition or internally generated thought.

1.6. Aims and outlines of the thesis

Semantic cognition supports different thoughts and behaviours. We can make sense of information from the external world, comprehending what we read or listen to (Keidel et al., 2018; Spitsyna et al., 2006), yet we also generate thoughts and memories that are independent of the external environment (Smallwood & Schooler, 2015; Zhang et al., 2022). Large-scale brain networks, including the DMN and the executive control network, play an important role in these distinct cognitive processes, and interact with each other to support both internally and externally driven processes (Esterman et al., 2014; Shao et al., 2024; Smallwood, Bernhardt, et al., 2021; Souter et al., 2024; Woolgar et al., 2011; Zhang et al., 2022). Using both behaviour and fMRI methods, this thesis aims to examine the behavioural and neural mechanisms that support the maintenance of task focus across different cognitive states. Across three different studies, we explore how memory representations, control processes and perceptual coupling dynamically interact to sustain coherent patterns of thought.

Study 1 (Chapter 2) examines the neural mechanism for sustaining focus on distinct cognitive states. Task focus is classically thought to be a product of top-down control (Kane & Engle, 2003; Miller & Cohen, 2001; Petersen & Posner, 2012); however, emerging evidence suggests that sustained focus during immersive reading or autobiographical memory

may rely less on executive regulation than on automatic, content-driven processing (Servais et al., 2023; Smallwood & Schooler, 2006). To examine the difference in sustaining focus on semantic and non-semantic tasks, the first experiment asked participants to perform comprehension (semantic) and arithmetic (non-semantic) tasks that varied in difficulty (Easy vs. Hard). Participants first generated personal thoughts linked to cue phrases (e.g., “Lottery win”) that triggered autobiographical retrieval during fMRI while participants either read factual sentences or solved arithmetic problems. After each trial, they were asked to provide their task focus rating. The hypothesis states that the arithmetic task might rely more on executive resources, which would lead to less focus during easy condition, as more resources are available for generating internal thoughts (Smallwood & Schooler, 2006); whereas the comprehension task might show more focus during easy condition, and engage semantic regions to maintain semantic representation (Binder et al., 2009). The second experiment replicated the paradigm to further examine whether similar mechanisms sustain focus across comprehension in both visual and auditory modalities, as well as during autobiographical memory retrieval with or without visual and auditory distractions. In this way, the study could investigate whether the modality of sensory inputs that are relevant or irrelevant to task demands modulate patterns of perceptual coupling and decoupling. Comprehension and autobiographical memory retrieval might recruit different DMN subsystems to maintain relevant memory representation to sustain a focussed state, as suggested by previous studies (Shao et al., 2024; Zhang et al., 2022). By modelling how fluctuations in attention shape neural activity, this study might reveal that sustained focus in externally and internally oriented cognition depends on different neural mechanisms across non-semantic, semantic and autobiographical memory tasks.

Study 2 (Chapter 3) examines the nature of ongoing thought at the behavioural level, especially in relation to mind-wandering. If semantic representation underpins task focus, then engagement is likely to be shaped by the content and structure of ongoing thought. To investigate whether difficult texts increase mind-wandering during reading, this study manipulated text difficulty in factual text comprehension and short story comprehension. Mind-wandering during reading might be induced more by difficult texts compared to easy

texts, and be associated with more drifting thoughts and worse text comprehension (e.g., Feng et al., 2013; Kahmann et al., 2022; Smallwood, 2011). In addition, the factual text comprehension might elicit more mind wandering than short stories, as it has been suggested that narratives provide a more immersive reading experience (Clinton et al., 2020; Mar et al., 2021). This study also explored patterns of ongoing thought during reading using MDES. MDES has been widely used to capture readers' ongoing experiences on multiple dimensions, including both on-task and off-task cognition (Turnbull, Wang, Murphy, et al., 2019; Wallace et al., 2025). This study might identify thought patterns that are related to greater mind-wandering, as well as thought patterns that reflect task-related thought contents, thereby revealing how thought patterns are differentially associated with comprehension of different types of texts. This study may help explain how the content of coherent ongoing thought during reading influences task focus.

Study 3 (Chapter 4) examines the function of perceptual coding in shaping the balance between externally oriented attention, semantic processing and internally generated cognition. The participants from the second experiment in Study 1 were asked to perform a retinotopic mapping task, to investigate the functional relevance of retinotopic coding for task focus during comprehension and autobiographical memory retrieval. Several studies have reported retinotopic coding in high-level cortical areas (Knapen, 2021; Silson et al., 2021; Szinte & Knapen, 2020), with the DMN showing selective deactivation as a function of visual stimuli position (Steel et al., 2024; Szinte & Knapen, 2020). Similarly, the distributed retinotopic coding may also be observed across the whole brain in our study. In addition to the negative retinotopic coding reported in previous work, given the DMN's role in integrating perceptual information, it may preserve positive retinotopic coding as well. Recent work shows that negative retinotopic coding embedded in high-order cortex may help to coordinate interactions between perceptual information and memory-based processes across the cortex (Steel et al., 2021; Steel et al., 2024). Using principal component analysis (PCA), this study identified large-scale patterns of retinotopic organization, and investigated their relationship with brain activity associated with focus. This study can reveal how individual differences in

visual organization relate to sustaining focus during both externally directed tasks (e.g., reading) and internally directed tasks (e.g., autobiographical memory retrieval tasks).

Overall, this thesis explores the behavioural and neural mechanisms for sustaining focus across different cognitive states, such as arithmetic, reading and autobiographical memory recall, by examining the dynamic interactions between representational systems, control processes, and perceptual coupling. Furthermore, this thesis will investigate whether individual differences retinotopic coding organization are associated with the neural activity in sustaining focus across externally and internally oriented tasks.

Chapter 2. Distinct neural architectures of focus: Memory-related engagement is associated with control disengagement

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2.1. Abstract

Prevailing models propose that sustained focus is a product of top-down control that amplifies task-relevant representations while suppressing distraction. We challenge this view, demonstrating that the neural signatures of mental focus differ across cognitive modes. In two neuroimaging studies, we used a paradigm that creates conflict between external task goals and self-generated thought, to identify the neural correlates of task focus in contexts varying in memory engagement. In Study 1, arithmetic and comprehension tasks were associated with distinct neural architectures of task focus: arithmetic-related focus recruited visual–motor regions, while comprehension-related focus was characterized by the recruitment of memory systems and reduced activation of control regions. Study 2 extended these findings, with both externally directed comprehension and internal memory retrieval associated with a shared neural profile of reduced control engagement, despite reliance on distinct memory systems. Furthermore, focus covaried with activity in heteromodal semantic regions across both reading and listening, suggesting semantic engagement is a primary marker of being on task during comprehension. Our findings indicate that sustained focus during memory-guided cognition is characterized by mutual disengagement between control and memory networks. This discovery motivates a departure from traditional executive-control accounts, since task focus in meaningful contexts is associated with the recruitment of representational structures in long-term memory rather than active top-down supervision.

2.2. Introduction

Task focus is conventionally viewed as a product of deliberate, top-down control (Kane & Engle, 2003; Miller & Cohen, 2001; Petersen & Posner, 2012). Yet, the brain can sustain remarkable focus during immersive memory recall with minimal apparent effort, challenging the assumption that task focus always depends on executive regulation. Prior work demonstrates that task engagement sharpens neural responses in relevant cortical regions and suppresses competing information by modulating the connectivity between control, sensory, and default mode networks (DMN; e.g., Cole et al., 2013; Fox et al., 2005; Spreng et al., 2013). However, this account cannot explain forms of sustained cognition that unfold independently of control networks. Here, we test whether the brain can maintain focus

through the self-organizing dynamics of memory systems, without continuous executive oversight.

A classic executive-failure hypothesis proposes that mind-wandering during externally oriented tasks such as reading reflects a breakdown in top-down control. When frontal–parietal control systems fail to prioritize task-relevant information, there is insufficient suppression of internally generated content within the DMN (Kane & McVay, 2012; McVay & Kane, 2010). The fronto-parietal control network (FPCN) maintains goal-relevant representations and typically responds more strongly when demands increase (Duncan, 2010; Fedorenko et al., 2013; Turnbull, Wang, Murphy, et al., 2019). Through its subregions, FPCN aligns functionally with either DMN or the dorsal attention network, thereby supporting internal and external modes of cognition (Dixon et al., 2018; Gonzalez Alam et al., 2022; Maillet et al., 2019; Murphy et al., 2020; Smallwood et al., 2012; Souter et al., 2024). This perspective predicts that higher focus should coincide with stronger control engagement.

The DMN, conversely, is classically assumed to deactivate in attention-demanding contexts (Greicius et al., 2003; Raichle, 2015), and to activate during unconstrained, self-generated thought (Andrews-Hanna, Smallwood, et al., 2014; Smallwood & Schooler, 2006). Yet a growing literature shows that DMN activity can accompany goal-directed cognition when memory retrieval or semantic comprehension is required (Krieger-Redwood et al., 2016; Zhang et al., 2022). Some cognitive states might also be sustained via memory-based systems: dorsomedial and core DMN subsystems are recruited during both text comprehension and autobiographical recall respectively, with stronger core DMN activation observed when participants are more focused on memory recall than comprehension (Chiou et al., 2020; Zhang et al., 2022). These patterns indicate that semantic engagement might be a common mechanism supporting focus across internally and externally oriented cognition (Zhang et al., 2019), and that memory networks are positively associated with task focus in some cognitive modes.

This perspective motivates a re-evaluation of the link between difficulty, control, and focus. Classical theories posit that harder tasks, which demand more attention, elicit greater

control engagement and less mind-wandering (McVay & Kane, 2010; Smallwood, 2013; Smallwood & Schooler, 2006). However, studies of reading comprehension reveal the opposite: people report more off-task thought when texts are difficult (Feng et al., 2013; Kahmann et al., 2022; Mills et al., 2015; Soemer et al., 2019). Thus, sustained focus on comprehension can be achieved in the absence of control when texts are easy to follow, motivating the hypothesis that semantic engagement may be key to cognitive focus during reading or listening, rather than attentional mechanisms that prioritize relevant sensory inputs.

To test these ideas, we conducted two functional MRI studies examining how large-scale brain networks support sustained focus across internal and external cognitive modes. In Study 1, participants performed externally oriented tasks -- arithmetic or sentence comprehension -- with each trial preceded by autobiographical memory cues, creating competition between task goals and self-generated thought. Trial-by-trial focus ratings allowed us to model how fluctuations in attention shape neural activity and network coupling. Study 2 extended and replicated these effects by comparing sentence comprehension and autobiographical memory retrieval tasks, presented either alone or in competition, across spoken and written modalities. This design enabled us to test whether similar mechanisms are associated with focus across semantic and memory-based states, and whether modality influences these processes. Across tasks, we define focus as the stability of task-relevant mental representations. While traditional models equate focus with top-down supervision, we propose that focus within semantic contexts reflects successful immersion in meaning-based representations.

Across analyses, we observed distinct neural pathways associated with focus depending on cognitive context. In Study 1, focus in arithmetic involved reduced engagement of memory regions, whereas comprehension-related focus involved deactivation of control regions. Study 2 showed that both comprehension and autobiographical memory retrieval were associated with greater reductions in control engagement at higher levels of focus, with comprehension additionally associated with reduced activity in core DMN regions. Heteromodal semantic regions were associated with higher focus across reading and listening tasks, indicating that representational rather than sensory systems covary with sustained

comprehension. Conjunction analyses across studies 1 and 2 confirmed consistent semantic activation and control deactivation during focused comprehension. Finally, bidirectional connectivity analyses revealed mutual decoupling between control and semantic regions during focused comprehension, consistent with a pattern in which memory-based systems coincide with more stable cognitive states in the absence of executive engagement. Together, these findings challenge traditional executive-control accounts, indicating that in some cognitive modes, sustained thought reflects the engagement of memory architectures rather than top-down supervision.

2.3. Materials and Methods

2.3.1. Participants.

In Study 1, we recruited 35 participants (26 females, 9 males, mean age = 20 years, range = 18-29 years). All were right-handed native English speakers, and had normal or corrected-to-normal vision. One was excluded because of big head movement (relative head motion > 0.3 mm). Therefore, the final sample of this analysis included 34 participants (25 females, 9 males, mean age = 20 years, range = 18-29 years).

In Study 2, we recruited 30 participants (24 females, 6 males, mean age = 20 years, range = 18-23 years). All were right-handed native English speakers, and had normal or corrected-to-normal vision, except for one who had amblyopia in the right eye. Four participants were excluded from the analysis, because there was insufficient data to model the parametric effect of task focus after excluding runs in which all trials had the same demeaned task focus rating for at least one of the conditions. Therefore, the final sample included 26 participants (20 females, 6 males, mean age = 20 years, range = 18-23 years).

In both studies, none of the participants had any history of neurological impairment, diagnosis of learning difficulty or psychiatric illness. All provided written informed consent prior to taking part. Participants were recruited through participant pools and paid for their time or awarded course credits. Ethical approval was obtained from the Research Ethics Committees of the Department of Psychology and York Neuroimaging Centre, University of York (Project number: Study 1 - P1501; Study 2 - P1406).

2.3.2. Task Design and procedure.

Both Studies 1 and 2 were adapted from Zhang et al. (2022). In Study 1, we employed a within-subjects 2×2 design manipulating task (Comprehension vs. Arithmetic) and difficulty (Easy vs. Hard). Participants generated thoughts linked to cue phrases (e.g., “Lottery win”) outside the scanner. Inside the scanner, participants retrieved personal thoughts from cue phrases for 3 s, and then either read factual sentences or added up numbers for 9 s (see Figure 2.1A for task illustration). After each comprehension or arithmetic trial, participants provided ratings on a scale from 1 (i.e., thinking about other things) to 7 (i.e., focusing on the meaning of the sentence or the ongoing addition) within 2 s, which measured the extent to which participants were focused on the current task.

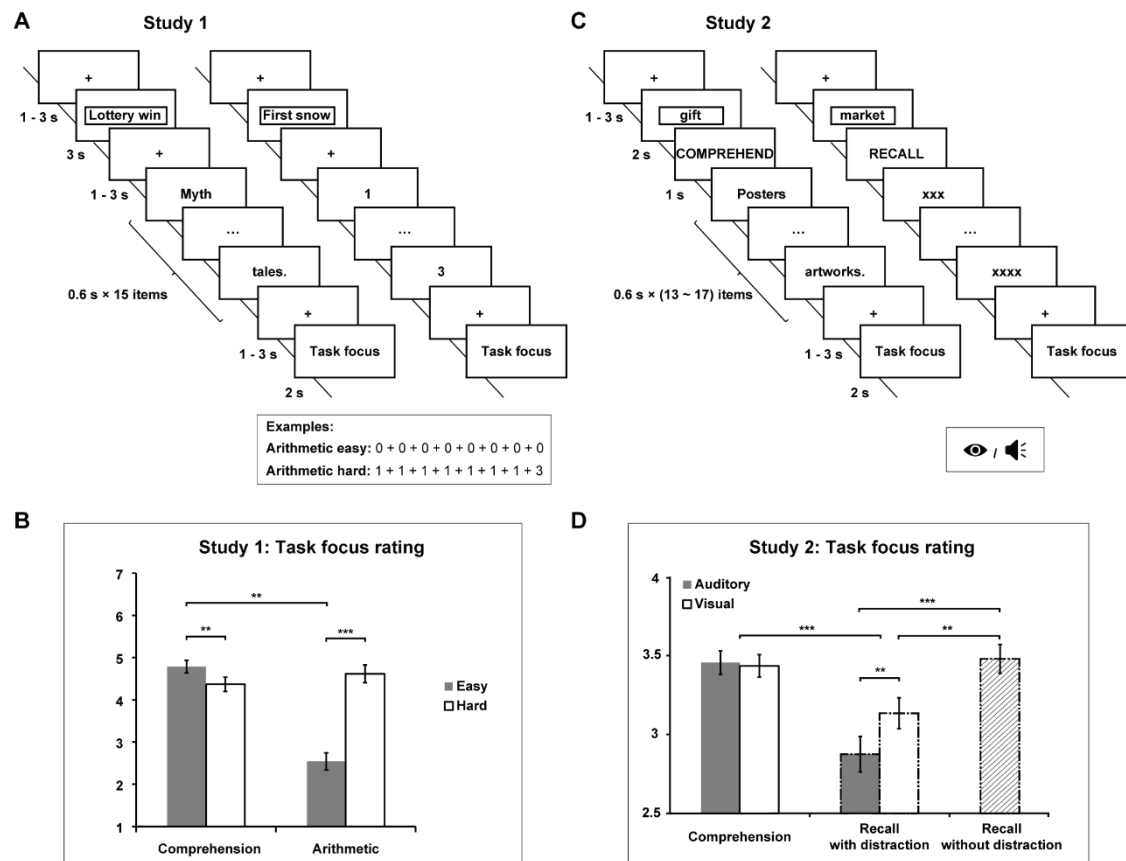


Figure 2.1 Task illustration and task focus ratings in two studies. (A) Task procedure in study 1. Participants retrieved personal thoughts linked to an autobiographical cue phrase (phrase with a box, e.g., “Lottery win”), then performed a comprehension or arithmetic task. At the end of each trial, participants rated their level of focus on a scale from 1 to 7. (B) Ratings of

task focus in study 1. The colour of solid bars indicates task difficulty (grey, easy; white, hard). Error bars represent the standard error of the mean (SE). (C) Task procedure in study 2. Participants recalled personal memories from a cue word (word with a box, e.g., “gift”) in the scanner, and then performed either a comprehension or recall task. In the comprehension task, participants read or listened to factual sentences. In the recall task, participants recalled personal memories while ignoring visual or auditory sentences, or without distraction. At the end of each trial, participants rated their level of focus on the intended task on a scale from 1 to 4. (D) Ratings of task focus in study 2. The colour of solid bars represents the sentence modality (grey, auditory; white, visual). The grid bar represents focus during recall without distraction. Error bars represent the standard error of the mean (SE). *** $p < 0.001$, ** $p < 0.01$, Bonferroni corrected.

Study 2 took place across two days. On day 1, participants generated personal memories linked to cue words (e.g., gift) outside the scanner. On day 2, inside the scanner, participants brought to mind their detailed personal memories related to a written and spoken autobiographical memory cue word for 2 s. Following the task instruction (i.e., COMPREHEND or RECALL) presented for 1 s, participants were asked to either comprehend the sentences (presented visually or auditorily), or recall their memories for the cue word for an average of 9 s. The experiment consisted of the following conditions: (a) visual sentences; (b) auditory sentences; (c) retrieve personal memories while ignoring visual sentences; (d) retrieve personal memories while ignoring auditory sentences; (e) retrieve personal memories (no distracting sentence presented; see Figure 2.1C for task illustration). After each trial, task focus ratings on a scale of 1 (i.e., not at all focused) to 4 (i.e., highly focused) were collected within 2 s to index the extent to which participants were able to focus on each task condition. For more information, refer to Appendices, Supplemental Methods.

2.3.3. Materials.

Study 1 included 50 paired topic sentences, which therefore resulted in two experiment versions, each containing 25 easy and 25 hard sentences. The versions were counterbalanced across participants. These sentences contained accessible factual content on non-emotive topics, with easy texts selected from BBC Bitesize and hard texts selected from

Wikipedia. For example, the topic MYTH included an easy version, “Myths are ancient tales filled with magical creatures, gods and mystery that are passed down the generations and not based on facts or reality”, whereas the hard version was, “Myth is a genre of folklore or theology consisting primarily of narratives that play a fundamental role in society such as foundational tales”. We balanced the number of characters across the easy and hard conditions (for all paired *t*-test, Bonferroni-corrected $p > .05$), to ensure that the visual loadings were comparable across conditions. Overall, the easy sentences were rated as significantly easier to understand, more interesting, more frequent, and they contained more words than the hard sentences (for detailed information, refer to Appendices, Supplemental Methods). For the arithmetic task, the easy condition consisted of additions of zeros, whereas the hard condition involved additions with random numbers between 1 and 4. To induce a mind wandering state prior to each comprehension or arithmetic trial, we presented a cue phrase before each sentence. A total of 25 cue phrases were selected from the positive set used in (ref. Schlagman & Kvavilashvili, 2008) (e.g., “Stars at night”, “Lottery win”). The same cue phrases were used across all conditions and were counterbalanced across runs to ensure that no phrase was repeated within the same run.

Study 2 presented participants with 96 sentences, all of which were preceded by a cue word. The sentences were selected using 96 highly frequent and concrete nouns as key words as a search term in Wikipedia to identify text that described largely unfamiliar facts about each item (sentence length: Mean $\pm$ SD = 20.33 $\pm$ 1.54 words). These sentences contained accessible factual content, on non-emotive topics; for example, “Posters are used for reproductions of artwork, particularly famous works, and are cheaper compared to the original” for the keyword POSTER. Overall, the sentences were unfamiliar, easy to understand and did not differ in familiarity and comprehensibility between conditions (for detailed information, refer to Appendices, Supplemental Methods). The cue words were 60 highly frequent and concrete nouns and were repeated twice across the whole experiment. The cue words were matched for lexical frequency and concreteness across conditions. The full set of sentences for both studies 1 and 2 is available on OSF (https://osf.io/cqbhv/overview?view_only=ea533ec03ad3471a8336cc32107c15f6).

2.3.4. fMRI data acquisition.

Whole brain structural and functional MRI data were acquired using a 3T Siemens MRI scanner utilizing a 64-channel head coil, tuned to 123 MHz at the York Neuroimaging Centre, University of York. We used a multiband-multi-echo (MBME) EPI sequence with the following parameters: TR=1.5 s; TEs = 12, 24.83, 37.66 ms; 48 interleaved slices per volume with slice thickness of 3 mm (no slice gap); FoV = 24 cm (resolution matrix = 3x3x3; 80x80); 75° flip angle; volumes per run below; 7/8 partial Fourier encoding and GRAPPA (acceleration factor = 3, 36 ref. lines; multi-band acceleration factor = 2). Structural T1-weighted images were acquired using an MPRAGE sequence (TR = 2.3 s, TE = 2.26 s; voxel size = 1x1x1 isotropic; 176 slices; flip angle = 8°; FoV= 256 mm; interleaved slice ordering). In Study 1, tasks were presented across four runs, each lasting 8.5 min, with 340 volumes in each run. In Study 2, tasks were presented across four runs, each lasting 9.35 min, with 374 volumes in each run.

2.3.5. Multi-echo data pre-processing.

The same preprocessing pipeline was applied to both Study 1 and Study 2. A MBME sequence was used to optimize signal from the anterior and medial temporal regions, while maintaining optimal signal across the whole brain (Halai et al., 2014) . We used TE Dependent ANALysis (TEDANA; version v23.0.1) to combine the images (DuPre et al., 2021; Kundu et al., 2013; Kundu et al., 2012). Anatomical pre-processing (fsl_anat; https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/fsl_anat) included re-orientation to standard MNI space (fslreorient2std), automatic cropping (robustfov), bias-field correction (RF/B1 – inhomogeneity-correction, using FAST), linear and non-linear registration to standard-space (using FLIRT and FNIRT), brain extraction (using FNIRT, BET), tissue-type segmentation (using FAST) and subcortical structure segmentation (FAST). The multi-echo data were pre-processed using AFNI (<https://afni.nimh.nih.gov/>), including de-spiking (3dDespike), slice timing correction (3dTshift; heptic interpolation), and motion correction (3dvolreg applied to echo 1 to realign all images to the first volume; these transformation parameters were then applied to echoes 2 and 3; cubic interpolation). The script used to implement the preprocessing

TEDANA pipeline is available at OSF

(https://osf.io/cqbhv/overview?view_only=ea533ec03ad3471a8336cc32107c15f6).

2.3.6. fMRI data analysis.

Individual level analysis was conducted using FSL-FEAT version 6 (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl; ref. Jenkinson et al., 2002; Smith et al., 2004; Woolrich et al., 2009). Denoised optimally-combined time series data were submitted to FSL. Pre-processing included high-pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with $\sigma = 100$ s), linear co-registration to the corresponding T1-weighted image and to MNI152 standard space (Jenkinson & Smith, 2001), spatial smoothing using a Gaussian kernel with full-width-half-maximum (FWHM) of 6 mm, and grand-mean intensity normalization of the entire 4D dataset by a single multiplicative factor. Pre-processed time series data were modelled using a general linear model correcting for local autocorrelation (Woolrich et al., 2001).

In Study 1, six Explanatory Variables (EV) of interest and four of no interest were modelled using a double-Gaussian hemodynamic response gamma function. The six EVs of interest were as follows: (1) easy comprehension; (2) hard comprehension; (3) easy arithmetic; (4) hard arithmetic; (5-6) task focus effect of comprehension and arithmetic as a parametric regressor. EVs of no interest were: (7) memory cue phrase; (8) fixation before sentences or numbers; (9) fixation before the rating question; (10) rating decision period. In Study 2, ten Explanatory Variables (EV) of interest and four of no interest were modelled using a double-Gaussian hemodynamic response gamma function. The ten EVs of interest were as follows: (1) visual sentence; (2) auditory sentence; (3) autobiographical memory while ignoring visual sentences; (4) autobiographical memory while ignoring auditory sentences; (5) autobiographical memory with no distracting sentence presented; (6-10) task focus effects for each of the five experimental conditions as a parametric regressor. EVs of no interest were: (11) memory cue word; (12) task instruction; (13) fixation (the period before the rating question); (14) rating decision period. No motion parameters were included in the models, as the data had already been denoised as part of the TEDANA pipeline (Kundu et al., 2012). EVs for each condition commenced at the onset of the first word of the sentence or the

first number, with EV duration set as the presentation time (e.g., 9 s in Study 1, or the entire length of the sentence in Study 2). The parametric EVs for the effect of task focus had the same onset time and duration for each trial in the EVs corresponding to the comprehension and arithmetic trials, and the demeaned task focus rating as the weight. Runs in which all trials within a condition had the same task focus rating value were excluded from analyses, since it was impossible to model the effects of task focus. This resulted in the removal of four participants' data in Study 2; on average, more than 77% of the data from Study 2 was retained across participants. The fixation period between trials provided the implicit baseline. In the group-level analysis, clusters were corrected using a threshold of $z = 3.1$ to define contiguous clusters and a familywise-error-corrected (FWE) significance level of $p < .05$.

Psychophysiological interaction (PPI) analyses were conducted separately for Study 1 and Study 2 using seeds derived from conjunction analyses. The model included all the regressors from the basic GLM model described above, a PPI term for each experimental focus effects, as well as the time series of the seed, using the generalized psychophysiological interaction (gPPI) approach (McLaren et al., 2012). The regressors were not orthogonalized. All Brain figures were visualized using BrainNet Viewer (Xia et al., 2013).

2.4. Results

2.4.1. Study 1: Differential focus effects during semantic and non-semantic tasks

Study 1 examined how task focus is sustained across semantic and non-semantic contexts to test the hypothesis that these distinct modes of cognition are sustained in different ways. In a within-subjects design ($N=34$), participants performed comprehension (semantic) and arithmetic (non-semantic) tasks that varied in difficulty (Easy vs. Hard; see Materials and Methods). Prior to scanning, participants generated personal thoughts linked to cue phrases (e.g., "Lottery win") to induce internally oriented, memory-based distraction. These cues were designed to trigger autobiographical retrieval during fMRI while participants either read factual sentences or solved arithmetic problems (serial addition). After each trial, participants rated their task focus on a 1–7 scale (1 = thinking about other things; attention fully diverted from task, 7 = thoughts fully on task; Figure 2.1A).

2.4.1.1. Behavioural results

A repeated-measures ANOVA examining task focus ratings explored the effects of task (comprehension/arithmetic) and difficulty (easy/hard). This revealed main effects of task ($F(1, 33) = 54.08, p < .001, \eta^2 = .62$), difficulty ($F(1, 33) = 27.47, p < .001, \eta^2 = .45$), and a task-by-difficulty interaction ($F(1, 33) = 58.60, p < .001, \eta^2 = .64$) (Figure 2.1B). Post-hoc Bonferroni-corrected t -tests showed that participants were more focused on easy than hard comprehension ($t(33) = 3.348$, Bonferroni-corrected $p = .002$), and more focused on hard than easy arithmetic ($t(33) = -7.01$, Bonferroni-corrected $p < .001$).

This behavioural dissociation suggests that the mechanisms sustaining task focus differ across domains. In the arithmetic task, participants achieve higher focus during harder trials by actively suppressing mind-wandering to meet task demands. In contrast, comprehension relies on engagement of the semantic system: focus is higher in easier texts, where visual-semantic processing more effectively stabilizes attention on the material.

2.4.1.2. Parametric effects of task focus in comprehension and arithmetic

To identify neural responses associated with subjective fluctuations in focus, we implemented a univariate general linear model (GLM; see Materials and Methods). Task difficulty was modelled categorically, while trial-by-trial ratings of task focus were entered as a parametric regressor across all trials. This approach isolated neural activity that covaried with moment-to-moment variation in focus, independent of mean activation differences between easy and hard conditions (see below; Figure 2.2). Main effects of task are shown in Appendices, Figure S2.1. Supplementary analyses confirmed highly similar effects of focus in the hard and easy trials of both tasks when these were analysed separately, and no significant differences in focus effects between hard and easy trials for either task (Appendices, Figure S2.2).

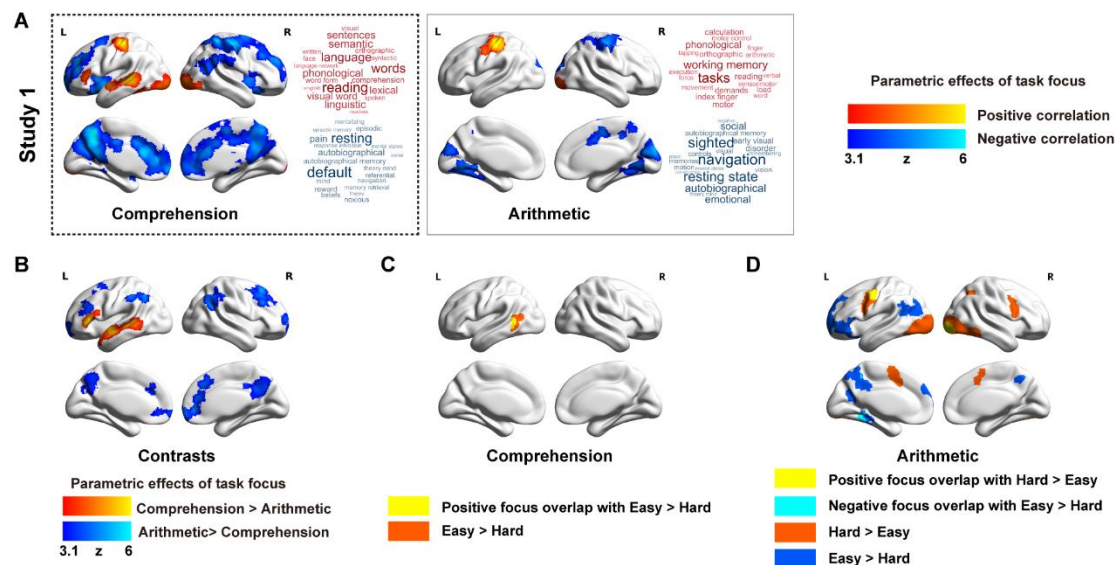


Figure 2.2 Parametric effects of task focus in Study 1. (A) These brain regions showed greater activation (red) or greater deactivation (blue) when participants reported better focus on the comprehension or arithmetic task. The word clouds indicate cognitive decoding of each map using Neurosynth: the font size of each item illustrates its importance, and the colour indicates its association (red = positive correlation, blue = negative correlation). (B) A comparison of regions showing greater focus effect during comprehension (red) or arithmetic task (blue). (C) Overlap between focus effect and task difficulty during comprehension. Red indicates regions showing greater activation during easy compared to hard comprehension. Yellow indicates regions associated with increased focus overlap with those more active during easy trials. (D) Overlap between focus effect and task difficulty during arithmetic. Red indicates regions showing greater activation during hard compared to easy arithmetic; dark blue indicates the opposite. Yellow indicates regions associated with increased focus overlap with those more active during hard trials, while bright blue indicates regions associated with decrease focus overlap with those more active during easy trials. Source data of unthresholded focus effect maps in A-B are available at NeuroVault (<https://neurovault.org/collections/UXFXQCND/>).

To examine how focus-related neural patterns map onto large-scale brain networks, we assessed the voxel-level overlap between thresholded focus activation maps and the 17-

network parcellation defined by Yeo et al. (2011). Networks were split by hemisphere to capture potential lateralization effects, given the left-lateralization of semantic cognition. Results are shown in Appendices, Figure S2.3, with separate bars for each hemisphere and colours indicating different networks. To simplify visualization, networks with fewer than 100 overlapping voxels are grouped as “other” (all networks are shown in OSF; https://osf.io/cqbhv/overview?view_only=ea533ec03ad3471a8336cc32107c15f6).

Greater focus during comprehension was associated with increased activation in the bilateral occipital cortex, left precentral/postcentral gyrus, inferior frontal gyrus (IFG), middle temporal gyrus (MTG), superior temporal gyrus (STG), and inferior temporal regions; see Figure 2.2A. Using Neurosynth (Yarkoni et al., 2011), we performed meta-analysis to reveal functional associations with these regions. Cognitive decoding of the focus map for comprehension identified terms such as “reading”, “words”, and “language”. These regions fell largely within visual, somatomotor, auditory and left-lateralized dorsomedial DMN networks, as defined by the Yeo et al. (2011) parcellation of intrinsic connectivity (see Appendices, Figure S2.3).

Higher focus during comprehension also elicited greater deactivation in the bilateral anterior and posterior cingulate, precuneus, insula, frontal pole, superior frontal gyrus (SFG), middle frontal gyrus (MFG), and right lateral parietal cortex; Figure 2.2A. Cognitive decoding of this map identified terms associated with “default”, “resting”, and “autobiographical” as well as “pain”, “noxious” and “response inhibition”. These regions largely fell within bilateral core DMN, control, salience and dorsal attention networks (Appendices, Figure S2.3).

During the arithmetic task, higher focus was associated with increased activation in left precentral/postcentral gyrus and right occipital pole; cognitive decoding identified terms such as “tasks”, “working memory”, and “phonological” (Figure 2.2A). These areas fell in the left somatomotor and right visual network (Appendices, Figure S2.3). Higher focus was also associated with deactivation in the bilateral cuneal cortex, lingual gyrus, fusiform gyrus, precuneus, and right cingulate, precentral/postcentral gyrus, and associated with terms like

“navigation”, “sighted”, “resting” and “autobiographical”. These areas of deactivation were largely within bilateral visual network and right SMN.

This analysis confirms distinct patterns of network engagement during task focus for comprehension and arithmetic. Focused comprehension elicits increased activation of semantic regions within the dorsomedial DMN subsystem, plus deactivation of the core DMN, control, and salience networks. In contrast, focused arithmetic is associated with greater engagement of occipital pole and motor cortex, and deactivation of medial occipital, temporal and parietal cortex.

To examine differences in the focus effect between comprehension and arithmetic, we conducted contrast analyses. As shown in Figure 2.2B, the left lateral temporal gyrus and IFG showed stronger focus effects during comprehension, whereas bilateral paracingulate gyrus, precuneus cortex, angular gyrus (AG) supramarginal gyrus (SMG), MFG/SFG, frontal pole and right cingulate gyrus showed stronger focus effects during arithmetic.

2.4.1.3. Effects of difficulty in comprehension and arithmetic

Next, we examined whether the neural effects of task focus overlapped with those of difficulty within each domain. In the arithmetic task, regions of motor cortex associated with increased focus also showed greater activation for difficult relative to easy trials, while regions linked to lower focus (characterized by more off-task thought) overlapped with DMN areas that were more active during easy trials (Figure 2.2D). This alignment suggests that focus and difficulty in the arithmetic task depend on shared mechanisms: sustaining attention requires engagement of visual–motor systems and suppression of default mode activity, both of which intensify as task demands increase. In contrast, regions associated with increased focus in comprehension overlapped with those more active during easy than hard trials in posterior temporal cortex (Figure 2.2C). This implies that sustained focus in reading is not a function of increased effort and might instead reflect successful engagement of temporal lobe semantic regions.

2.4.2. Study 2: Effects of focus in comprehension versus autobiographical memory recall

Study 1 revealed that sustained focus in externally oriented cognition is associated with different neural mechanisms across semantic and non-semantic tasks: comprehension engaged memory systems while suppressing control regions, whereas higher focus on arithmetic was associated with sensory-motor activity. In Study 2, we asked whether similar effects occur during internally directed cognition, and whether the mechanisms associated with task focus generalize across internal and external modes of thought. Participants alternated between comprehension and autobiographical memory retrieval tasks presented either alone or in competition, allowing us to test whether sustaining focus is associated with a shared neural process of control disengagement, irrespective of the sensory modality or the type of memory organizing cognition.

Twenty-six participants took part in Study 2, which was adapted from a previous task paradigm (Zhang et al., 2022). On day 1, participants generated personal memories linked to cue words (e.g., gift) outside the scanner. On day 2, in the scanner, participants were asked to either comprehend the sentences (presented visually or auditorily) or recall their memories for the cue word. The experiment consisted of the following conditions: (1) visual sentences; (2) auditory sentences; (3) retrieve personal memories while ignoring visual sentences; (4) retrieve personal memories while ignoring auditory sentences; (5) retrieve personal memories (no distracting sentence presented; see Figure 2.1C for task illustration). After each trial, task focus ratings were collected on a scale of 1 (i.e., not at all focused) to 4 (i.e., highly focused), indexing the extent to which participants were able to focus on each task condition.

2.4.2.1. Behavioural results

Repeated-measures ANOVA on the task focus ratings revealed higher focus in comprehension than recall ($F(1,25) = 17.06, p < .001, \eta^2 = .41$). There was a main effect of modality ($F(1,25) = 7.00, p = .014, \eta^2 = .22$), and a significant task-by-modality interaction ($F(1,25) = 7.95, p = .009, \eta^2 = .24$; Figure 2.1D). Post-hoc Bonferroni-corrected t -tests revealed higher focus when ignoring visual than auditory sentences during recall ($t(25) = -3.36$, Bonferroni-corrected $p = .003$), but no modality differences during comprehension ($t(25) = 0.37$).

A comparison of the three recall conditions (i.e., retrieving personal memories while ignoring auditory sentences, ignoring visual sentences, or with no distracting sentences presented), revealed a significant main effect of condition ($F(2,23) = 20.93, p < .001, \eta^2 = .46$). Participants were more focused during recall without distraction, relative to ignoring auditory ($t(25) = 5.36$, Bonferroni-corrected $p < .001$) or visual sentences ($t(25) = 3.94$, Bonferroni-corrected $p = .002$).

2.4.2.2. Parametric effect of focus ratings

We performed a univariate fMRI analysis to identify the parametric effects of focus ratings on the BOLD response. In the model, the five conditions (i.e., visual sentence, auditory sentence, autobiographical memory while ignoring visual sentences, autobiographical memory while ignoring auditory sentences, autobiographical memory with no distracting sentence presented) were included as five Explanatory Variables (EV) of interest, along with the parametric effect of focus for each condition (see Materials and Methods). Main effects of each task condition are shown in Appendices, Figure S2.4.

As shown in Figure 2.3, greater focus during auditory comprehension was associated with increased activation in semantic areas, including left anterior superior temporal sulcus/gyrus (aSTS/STG) and posterior middle temporal gyrus (pMTG). Greater focus during visual comprehension was similarly associated with increased activation in STG, as well as in bilateral inferior temporal regions such as ventral occipitotemporal cortex (vOT). Using Neurosynth, we performed meta-analysis to reveal functional associations with these regions. Cognitive decoding of the focus map for auditory comprehension identified terms such as “speech”, “auditory” and “comprehension”, while decoding the map for visual comprehension identified terms such as “reading”, “comprehension”, and “words”. More focus in auditory comprehension was associated with greater activation in the dorsal medial DMN subsystem and auditory network, while stronger focus on visual comprehension elicited greater activation in the dorsal medial DMN subsystem, dorsal attention network (DAN) and auditory network.

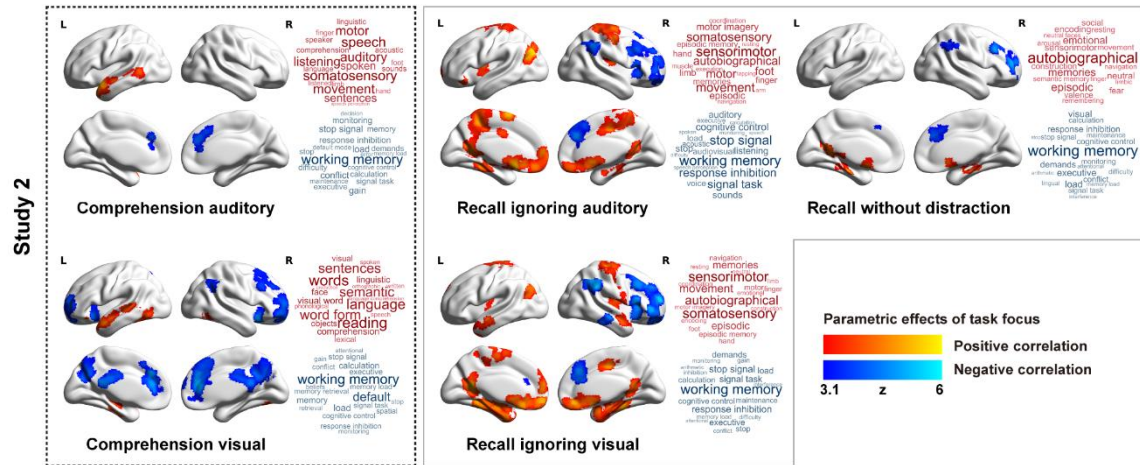


Figure 2.3 Parametric effects of task focus in Study 2. These brain regions show greater activation (red) or greater deactivation (blue) when participants reported better focus on the task. The word cloud indicates the cognitive decoding of the map using Neurosynth. In the word clouds, the font size of each item illustrates its importance, and the colour indicates its association (red = positive correlation, blue = negative correlation). Unthresholded maps of the focus effect, which were used for the Neurosynth decoding analysis, are available at NeuroVault (<https://neurovault.org/collections/UXFXQCND/>).

Higher focus also elicited greater deactivation in bilateral anterior cingulate and paracingulate cortex for both auditory and visual comprehension. Increased focus on visual comprehension elicited more extensive deactivation in bilateral posterior cingulate, frontal pole, insula, right SFG and MFG. Cognitive decoding of these focus effects for auditory and visual comprehension identified terms such as “working memory” and “inhibition”. Deactivation associated with higher task focus in comprehension therefore largely fell within the control and salience networks, irrespective of input modality, in line with the findings of Study 1.

During memory retrieval, there were positive parametric effects of focus in different brain regions to the comprehension tasks. The effects of focus on memory retrieval were similar for auditory and visual distraction, with increased activation when participants were more focused in bilateral anterior and posterior cingulate, parahippocampal and fusiform cortex, insula, postcentral and precentral gyrus, left superior lateral occipital cortex, SFG and

right supplementary motor cortex. Cognitive decoding of these maps identified terms associated with “sensorimotor”, “autobiographical” and “episodic” processing. Higher focus during memory retrieval without external distraction was associated with more constrained activation in bilateral parahippocampal and fusiform cortex, and left precuneus and posterior cingulate; these regions are associated with terms such as “autobiographical”, “episodic” and “memories” when decoded using Neurosynth. This focus-related activation was mainly in the core and medial temporal DMN subsystems and somatomotor network.

Greater focus in memory retrieval was also associated with increased deactivation across all three memory conditions in right AG and SMG, SFG, MFG, IFG, insula and frontal pole. Cognitive decoding revealed that these regions were associated with terms like “working memory”, “response inhibition” and “cognitive control”. This deactivation fell within control and salience networks. When there was no distraction, the overall response was reduced, but activation still fell within the medial temporal DMN subsystem, while the control network and the salience network showed deactivation.

Taken together, increased focus across comprehension and recall elicited greater deactivation in executive networks (i.e., control and salience), with activation patterns that varied according to the process engaged (i.e., comprehension, recall).

2.4.3. Conjunctions of focus effects across Study 1 and Study 2

Conjunction analyses examined whether the patterns of activation and deactivation during focused comprehension overlapped across datasets. We also asked whether focused comprehension and recall recruited regions that were disengaged by task focus in non-semantic tasks, such as arithmetic. Conjunction analyses used a z-statistic threshold of 2.6 and a FWE threshold of $p < 0.05$, in line with previous studies (Gonzalez Alam et al., 2025; Vatansever et al., 2021). Results are shown in Figure 2.4.

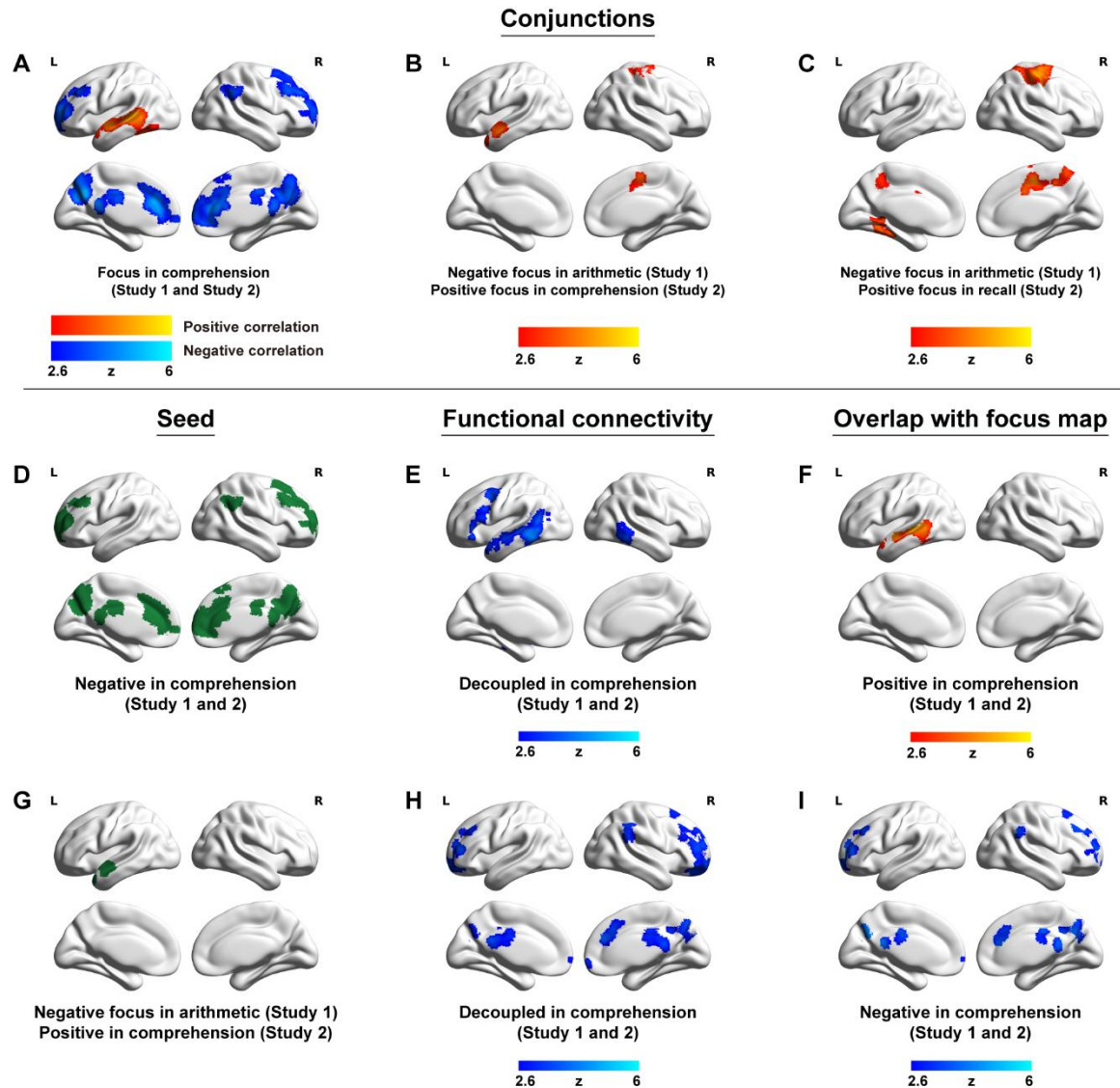


Figure 2.4 Conjunctions and task based functional connectivity. (A) Formal conjunction of focus effects for comprehension tasks in both Study 1 and Study 2, conducted using FSL “easythresh_conj” tool. Study 1 shows the effect of higher focus in reading, while Study 2 uses the main effect of higher focus in comprehension across visual and auditory modalities. These regions showed greater activation (red) or deactivation (blue) when participants reported better focus during comprehension. (B) The conjunction of negative focus effects during arithmetic in Study 1 and positive focus effects during comprehension in Study 2. Warm colours indicate regions with greater deactivation when participants reported higher focus during arithmetic in Study 1, and greater activation when participants reported higher focus during comprehension in Study 2. (C) The conjunction of negative focus during arithmetic in Study 1 and positive focus effects during recall in Study 2. Warm colours

indicate regions with greater deactivation when participants reported higher focus during arithmetic in Study 1, and greater activation when participants reported higher focus during recall in Study 2. (D) Seed included regions showing greater deactivation with higher focus during comprehension across Studies 1 and 2. (E) PPI map from (D, seed), showing regions (blue) with increased decoupling when focus was higher. (F) Overlap of (E) with conjunction focus map, highlighting that these regions (red) also showed greater activation when comprehension focus was high. (G) Seed showing greater activation with higher focus in comprehension (Study 2). (H) PPI map from (G, seed), showing regions (blue) with greater decoupling during high focus. (I) Overlap of (H) with conjunction focus map, highlighting that these regions (blue) also showed greater deactivation when comprehension focus was high. Source data of unthresholded maps in (A) – (C), (E) and (H) are available at NeuroVault (<https://neurovault.org/collections/UXFXQCND/>).

The conjunction of focused comprehension across Studies 1 and 2 (Figure 2.4A) revealed common areas of increased activation in left vOT and MTG/STG, and deactivation in bilateral anterior and posterior cingulate, paracingulate gyrus, precuneus, frontal pole, MFG and right SFG, AG/SMG. When participants were more focused on comprehension, there was a reliable pattern of increased activation in lateral semantic regions, and decreased activation in the core DMN and executive regions.

A conjunction of negative focus during arithmetic in Study 1 and positive focus in comprehension (across modalities in Study 2; Figure 2.4B) revealed overlap in left anterior temporal lobe and right precentral/postcentral gyrus and supplementary motor cortex. We compared this conjunction map with a meta-analytic map from Neurosynth (Yarkoni et al., 2011) for the term ‘semantic’ (1031 contributing studies), which revealed overlap in left ATL (Figure 2.4G). Therefore, semantic regions are engaged during focused comprehension, and are suppressed during arithmetic, which does not require access to the semantic store.

The conjunction of negative focus during arithmetic in Study 1 and positive focus during recall in Study 2 (Figure 2.4C) further revealed bilateral precuneus, right precentral/postcentral gyrus, SPL, and supplementary motor cortex, and left parahippocampal

gyrus/occipitotemporal regions. The left parahippocampal gyrus, occipitotemporal cortex and precuneus overlapped with the Neurosynth meta-analytic map for ‘episodic’ (488 contributing studies). These results indicate that regions associated with episodic memory are engaged during focused recall and suppressed when participants focus on arithmetic.

2.4.4. Effects of focus on functional connectivity

Using conjunctions that highlighted the distinct roles of control and semantic memory systems in task focus as seeds, we performed psychophysiological interactions (PPI) across the whole brain to investigate variation in connectivity as a function of focus across tasks. We seeded control, salience and default mode network regions that deactivated during more focused comprehension across studies (blue regions in Figure 2.4D). We also seeded memory-related regions in ATL (Figure 2.4G), which overlapped with the meta-analytic maps for ‘semantic’; activation in this site increased with focus during comprehension and decreased for arithmetic. We constructed separate PPI models for these two seeds and examined the parametric effect of task focus on connectivity in Studies 1 and 2 separately. The PPI models included all the regressors in the basic GLM model, a PPI term for each focus effect, as well as the time series of the seed (for details, See Materials and Methods), using the generalized psychophysiological interaction (gPPI) approach (McLaren et al., 2012). The regressors were not orthogonalized. The two datasets revealed similar patterns, and we focus on effects observed reliably across both studies below (see Appendices, Figure S2.5 for all PPI results).

The first seed, showing deactivation in focused comprehension in medial and frontal regions (Figure 2.4D), showed greater functional segregation with bilateral MTG/ITG, and left lateral frontal cortex (IFG, precentral gyrus, MFG) when comprehension focus was higher (see Figure 2.4E). The overlap (Figure 2.4F) of these PPI results with the conjunction map for focus effects in comprehension (brain map in Figure 2.4A) demonstrates that control and core DMN areas become increasingly decoupled from regions supporting focused comprehension, suggesting this pattern of disengagement occurs when semantic systems maintain attention with minimal interference.

The second seed, in left ATL, showed greater activation when participants reported higher focus during comprehension (Figure 2.4G). As focus increased, the ATL became more functionally segregated from areas in bilateral MFG, frontal pole, precuneus, right anterior cingulate/paracingulate gyrus, SFG, and SMG across Studies 1 and 2 (Figure 2.4H). Masking the conjunction focus map with this PPI highlighted the same restricted set of regions largely in control networks (Figure 2.4I), which showed deactivation during focused comprehension. These results suggest that focus is associated with functional segregation of language and semantic regions from control and core DMN networks. Together with the first seed, these results demonstrate bidirectional disengagement between semantic and control regions during focused comprehension, regardless of which network is seeded.

2.5. Discussion

Our findings across two independent studies challenge accounts in which sustained focus is primarily a product of executive control. Instead, the neural correlates of task focus were found to vary across cognitive modes, with meaning-based contexts associated with reduced control-network activity and greater functional segregation between control and memory systems. Participants performed externally oriented tasks (comprehension or arithmetic) preceded by autobiographical cues, creating competition between task goals and self-generated thought, and rated their focus after each trial. In Study 1, focus during arithmetic was associated with visual–motor regions, while focused comprehension was associated with greater engagement of semantic regions and reduced activity in control and salience networks. In Study 2, comprehension and autobiographical memory showed convergent patterns: focused cognition coincided with engagement of memory systems and reduced control involvement. In both studies, control and memory systems showed reciprocal separation when participants were more focused.

Functional separation of control and memory systems may be associated with a semantic “flow” state that is relatively independent of executive control. In this view, coherent thought may be sustained through intrinsic dynamics within memory systems. Rather than requiring continuous external regulation of goal-relevant representations by control networks, these systems may contain structural constraints—such as semantic

associations—that allow cognition to proceed along well-established pathways (Branzi & Lambon Ralph, 2023; Humphreys et al., 2015; Lanzoni et al., 2020). Thus, being “on task” during comprehension may reflect a handover from executive control to self-organizing memory systems, with thought sustained by the internal structure of the text’s meaning.

Executive networks are typically engaged during demanding tasks, amplifying relevant information and suppressing distraction (Corbetta & Shulman, 2002; Duncan, 2010; Favila et al., 2018; Fedorenko et al., 2013; Woolgar et al., 2011). Executive-failure accounts propose that lapses of attention arise when such control is insufficient, allowing internally generated thought to intrude (Kane & McVay, 2012; McVay & Kane, 2010). Yet stronger control recruitment does not always predict better performance: more erratic, error-prone (“out-of-the-zone”) behaviour can be associated with greater control activation (Esterman et al., 2014). Our findings refine this perspective. During arithmetic, higher focus was associated with visual–motor regions, whereas during semantic comprehension and memory retrieval it coincided with reduced engagement of control and salience networks, indicating distinct neural routes to focused cognition.

Behavioural studies indicate that the link between executive control and mind-wandering is more nuanced than simple executive-failure accounts suggest. In non-semantic tasks, mind-wandering typically decreases as difficulty increases, consistent with greater control demands (McKiernan et al., 2006; Smallwood & Schooler, 2006). In contrast, in semantic tasks such as reading, greater difficulty can increase mind-wandering (Forrin et al., 2019; Kahmann et al., 2022; Steindorf et al., 2023), potentially because disruption to semantic prediction and integration promotes internally generated thought. Under such conditions, semantic memory may decouple from sensory input, allowing internally driven associations to dominate over text-related processing. These dissociations suggest that the mechanisms supporting sustained attention differ across cognitive modes, depending on whether cognition is control-driven or representation-driven.

Our neural data help to explain these behavioural patterns and show they cannot be reduced to task difficulty alone. Focused comprehension was associated with reduced engagement of control and salience networks, together with weaker functional coupling

between these regions and lateral temporal cortex. If this pattern merely reflected lower executive demands, similar effects would be expected across tasks. Instead, arithmetic showed a partially opposing profile, with higher focus linked to greater engagement of visual–motor systems and stronger deactivation of memory-related regions. Within comprehension, parametric analyses further isolated trial-by-trial variation in focus independent of easy and hard task conditions, indicating that these neural signatures tracked attentional state rather than difficulty *per se*. Across studies, comprehension and autobiographical retrieval converged in linking higher focus to reduced control involvement despite differing task goals and stimulus contexts. Together, these findings suggest that sustained attention depends on cognitive mode: in some contexts, focus is linked to increased goal-directed processing, whereas in memory-guided cognition it coincides with reduced executive involvement and greater reliance on representational systems. This pattern points to a third attentional mode—neither passive mind-wandering nor effortful control—in which memory representations sustain coherent thought through a flow-like state of control disengagement.

Sustained comprehension across both reading and listening engaged the same heteromodal semantic and language regions in superior and middle temporal gyri. This modality-invariance indicates that task focus depends on representational coherence in long-term memory rather than attentional mechanisms tied to a specific sensory channel. Anterior STG was implicated in sustained focus in comprehension across modalities and in off-task thought during arithmetic, suggesting that this region underpins both task-relevant semantic retrieval and mind-wandering (Smallwood et al., 2016; Zhang et al., 2019). This site is proximal to the “semantic hub” proposed to integrate different modalities to give rise to coherent heteromodal concepts (Lambon Ralph et al., 2017), and it is implicated in both coupled and decoupled aspects of semantic cognition (Murphy et al., 2018). The similarity between reading, listening, and off-task thought during arithmetic likely reflects a role for heteromodal semantic representations in all these extended cognitive states, providing a shared basis for maintaining continuity of meaning over time.

We also observed clear dissociations between DMN subsystems across memory states. The dorsomedial DMN, linked to semantic cognition (Binder et al., 2009; Chiou & Lambon Ralph, 2019; Shao et al., 2024; X. Wang et al., 2020), was more engaged during focused comprehension across modalities, consistent with its role in conceptual coherence (Branzi & Lambon Ralph, 2023; Humphreys et al., 2015; Lanzoni et al., 2020). In contrast, the medial temporal and core DMN subsystems were more engaged during focused autobiographical memory retrieval: the MT subsystem is implicated in episodic memory and scene construction (Gonzalez Alam et al., 2025; Kravitz et al., 2011; Reagh & Yassa, 2014), while core DMN activates during autobiographical memory (Zhang et al., 2022) and self-relevant cognition (Andrews-Hanna, Smallwood, et al., 2014; Konu et al., 2020). Despite these differences, control-network suppression overlapped across conditions: dorsomedial prefrontal cortex showed deactivation with higher focus during reading, listening, and autobiographical retrieval, irrespective of distracting stimuli. This convergence suggests that although distinct DMN subsystems support different forms of memory retrieval, focused memory-based cognition consistently involves reduced executive involvement.

Several limitations should be noted. The present studies focused on arithmetic, comprehension, and autobiographical retrieval, and broader sampling of cognitive domains will be needed to determine how widely these modes generalize. Because fMRI provides correlational measures of neural activity, the observed patterns of network engagement and decoupling do not by themselves establish causal mechanisms (Bielczyk et al., 2019; Henson, 2005). In addition, self-reported focus likely reflects multiple processes, including motivation, effort, and subjective absorption (Grund et al., 2024; Smallwood & Schooler, 2015; Unsworth et al., 2024). Future work combining causal perturbation methods and temporally resolved imaging could clarify how control and memory systems interact across tasks.

The ability to maintain coherent, goal-directed thought without continuous executive supervision may be highly adaptive. Executive control is cognitively demanding and likely metabolically costly (Anderson & Green, 2001; Wiehler et al., 2022); by leveraging the self-organizing properties of long-term memory, the brain may sustain focus on meaningful information such as language or autobiographical memories more efficiently. This perspective

suggests that when past experience supports cognition, focus may often involve fluent processing within representational systems, with top-down control serving primarily as intermittent guidance or error correction rather than a continuous driver of thought.

Chapter 3. Mind-wandering content, not just frequency, predicts comprehension in narrative and factual reading

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3.1. Abstract

Mind-wandering is typically suppressed in demanding tasks, yet in reading, increased difficulty can instead promote off-task thought. Since semantic representations are engaged by both reading and internally-generated thought, reading may be especially sensitive to the alignment between ongoing thought content and task goals, with easier texts that allow more automatic semantic access suppressing mind-wandering. In two experiments, participants read factual texts and short stories that varied in difficulty, while self-caught mind-wandering was recorded, and multidimensional experience sampling was used to characterise patterns of ongoing thought. Across both text types, hard texts elicited more mind-wandering. Experience sampling identified four types of thoughts during reading: future problem solving, intrusive social thought, knowledge retrieval, and deliberate detail. The prevalence of these thought experiences varied across text difficulty and text type. Notably, task-unrelated future problem solving was associated with poorer comprehension, whereas deliberate detail was linked to better comprehension, particularly for factual texts. These findings suggest that reading comprehension depends not only on task difficulty but also on the alignment of ongoing thought with semantic goals, helping to explain why narrative texts are often easier to remain engaged with than factual materials.

3.2. Introduction

Mind-wandering is often described as a shift of attention away from the current task toward self-generated thought (Paul Seli et al., 2018; Smallwood & Schooler, 2006, 2015). A dominant assumption in the literature is that such off-task thought is more likely to occur when task demands are low, because spare executive resources are available to support internally-generated cognition (Smallwood & Schooler, 2006, 2015). Consistent with this view, studies frequently report higher rates of mind-wandering during relatively easy tasks (Forster & Lavie, 2009; Smallwood & Schooler, 2015). However, reading appears to be an exception to this pattern. Across multiple investigations, more difficult texts are associated with increased, rather than reduced, mind-wandering, and with poorer comprehension (Feng et al., 2013; Kahmann et al., 2022; Smallwood, 2011; Soemer et al., 2019). This contrast

raises an important question: why does reading show a different relationship between task difficulty and mind-wandering, compared with other cognitive tasks?

One possibility is that reading and internally-generated thought draw on overlapping semantic retrieval processes (Renoult et al., 2019; Smallwood et al., 2016; Vatansever et al., 2021; H.-T. Wang et al., 2020; Zhang et al., 2019). Successful comprehension requires the construction of a coherent situation model, integrating incoming linguistic input with stored semantic knowledge (Graesser et al., 1994; Kintsch, 1988; Zwaan & Radvansky, 1998). At the same time, internally generated thought, which is a form of memory-based cognition, also draws on semantic knowledge and the integration of meaning over time (Moscovitch et al., 2016; Pacheco Estefan et al., 2019; Renoult et al., 2019; Vatansever et al., 2021; H.-T. Wang et al., 2020). When we read easy texts, semantic processing is thought to be tightly aligned to visual inputs and this may occur relatively automatically (Chiou & Lambon Ralph, 2016, 2019; Tyler et al., 2013; Zhang et al., 2022; Zhang et al., 2019). The Stroop effect, in which word meaning interferes with the goal of naming the ink colour, demonstrates this automatic semantic access from printed words. However, when texts become difficult, semantic access and integration are more effortful and error-prone, and competition may arise between externally-oriented comprehension and internally generated thought. From this perspective, mind-wandering during reading may not simply reflect a failure of executive control (McVay & Kane, 2010; McVay & Kane, 2012), but competition for shared semantic resources. In addition, unlike executive accounts, which are largely agnostic about the *content* of off-task thought, a semantic competition account predicts that the nature of ongoing thought should matter for comprehension, particularly when semantic processing is demanding.

Mind-wandering is not a unitary phenomenon. The content of spontaneous thought varies widely, from intrusive or distracting experiences -- for example, thinking about oneself in the past or future -- to deliberate, goal-directed, or knowledge-based thinking that might be relevant to an ongoing task even when it reduces attention to the immediate sensory input required by the task (Mulholland et al., 2023; Paul Seli et al., 2018). As a result, the associations between mind-wandering and task performance vary; while off-task thought is typically associated with poor focus and error-prone behaviour, it can also enhance creativity,

problem solving and episodic memory consolidation (Baird et al., 2012; Klinger, 2013; Schooler et al., 2011). This heterogeneity in the content and consequences of off-task thought may be especially relevant for reading, where some forms of self-generated thought could disrupt comprehension, while others, like retrieval of relevant knowledge, should support text understanding. Emerging theoretical accounts suggest that, during narrative reading, internally generated thought can contribute to the construction of rich mental simulations that are integral to comprehension (Fabry & Kukkonen, 2019).

Multidimensional experience sampling (MDES) characterises this variation in internally-generated thought (Smallwood et al., 2016; Smallwood, Turnbull, et al., 2021). MDES asks participants to describe their ongoing experiences on multiple dimensions (e.g. whether they involve future events, whether they are relevant to the task), and these data are then decomposed to identify thought patterns that vary across multiple dimensions. MDES has been shown to reliably capture both on-task and off-task cognition (Turnbull, Wang, Murphy, et al., 2019; Wallace et al., 2025) and it is sensitive to distinct brain states associated with different patterns of thought (Konu et al., 2020; McKeown et al., 2023; Smallwood, Turnbull, et al., 2021). Therefore, MDES is a useful technique to examine the relationship between different thought patterns and reading comprehension in different kinds of texts.

In the present study, we used MDES alongside self-caught mind-wandering reports to examine how text difficulty and text type shape patterns of ongoing thought during reading, and how these patterns relate to comprehension. Participants completed two reading experiments involving factual texts and short stories, each presented in easy and hard versions. We asked (i) whether difficult texts increase mind-wandering across reading contexts, (ii) if different types of texts elicit distinct patterns of thought, and (iii) whether specific thought patterns are differentially associated with comprehension of different types of texts. This approach allows us to test whether variation in reading comprehension reflects not only task difficulty, but the alignment between the content of ongoing thought and the semantic goals of the task.

3.3. Methods

3.3.1. Participants

We recruited 95 participants (74 females, 21 males; mean age $\pm$ SD = 20.4 $\pm$ 2.2 years, range = 18 – 29 years). 93 were native English speakers, and 2 spoke English fluently, having learned English before the age of 10. All participants had normal or corrected-to-normal vision. 6 participants reported reading problems that would not prevent them from completing the task.

Due to a software issue, one participant completed eight story texts and two factual texts, and another participant completed seven story texts and four factual texts; data from both participants were retained in the analysis. One participant was excluded from the analysis for failing to press the space bar (to indicate off-task thought) at all during the study. Based on reading time data available for a subset of participants ($n = 49$), two participants were excluded for not spending sufficient time reading the factual texts (average reading time < 15 s). Therefore, a total of 92 participants (71 females, 21 males; mean age $\pm$ SD = 20.5 $\pm$ 2.2 years, range = 18 – 29 years) were included in the final analysis. 49 participants were paid for their time or awarded course credits for their participation, and 46 participated voluntarily. Ethical approval was obtained from the Ethics Committee of the Department of Psychology, University of York.

3.3.2. Task design and materials

The current study consisted of two experiments: factual text comprehension and short story comprehension. Participants completed both experiments in a counterbalanced order. Both text types were presented in easy and hard versions. We examined mind-wandering during the reading of these texts in two ways: first, we recorded the number of self-caught occurrences of mind-wandering during reading; secondly, we examined the types of thoughts that occurred during reading using multidimensional experience sampling (MDES; Smallwood et al., 2016; Smallwood, Turnbull, et al., 2021). MDES included 16 questions focussed on different aspects of experience, which were rated on a scale from 1 to 10 (see Table 3.1).

All texts in this study were generated by ChatGPT-3.5. This approach allowed systematic manipulation of text difficulty while holding topic, length, and genre constant. For factual texts, difficulty was manipulated by specifying the intended level of reader expertise in the generation prompt, thereby varying semantic density and assumed background knowledge without changing topic content. For narrative texts, difficulty was manipulated by disrupting narrative coherence through pseudorandom sentence reordering, while preserving lexical content and overall length. All texts were matched for length and presented without headings or lists. Although generative language models may introduce uncontrolled stylistic variation, this approach was well suited to the present aims, which focused on how readers' ongoing thought patterns in a naturalistic task vary as a function of perceived difficulty and text type, rather than on fine-grained linguistic features.

For factual texts, we generated easy and hard conditions by generating texts aimed at a lay audience versus a final year undergraduate student. For example, for the topic *noctilucent clouds*, the prompt for the easy factual text was: *Create a 500-word encyclopaedia entry about noctilucent clouds, targeted towards a layperson with no prior knowledge on this topic, without lists and subheadings*. In contrast, the prompt for the hard factual texts was *...targeted towards final year undergraduate students writing an essay on this topic*.

For the story texts, we manipulated difficulty by varying the order of narrative sentences. For example, for the story about *Astronaut*, the easy text was generated with the prompt: *Create a 500-word short story about astronauts, targeted towards someone with a reading age of 21 years*. The hard story text was created by reordering the sentences pseudorandomly so that they were no longer in a logical sequence.

Three comprehension questions were generated for each text using ChatGPT. The prompt was: *Please generate multiple-choice reading comprehension-style questions specific to the below text extract*. For each text, ChatGPT generated three multiple-choice questions with four options, including one correct answer. To discourage guessing, a fifth response option ("I don't know") was added to each question.

In total, we generated sixteen factual texts (eight easy and eight hard) covering eight topics, and another sixteen story texts (eight easy and eight hard) linked to eight story topics.

These texts were divided into two experiment versions with no overlapping topics. Each version contained eight factual texts (four easy and four hard) and eight story texts (four easy and four hard). All texts contained around 500 words ($\pm 10\%$). The text versions, as well as the order of the factual and story comprehension experiments, were counterbalanced across participants (all materials are available on OSF: https://osf.io/3gmnt/overview?view_only=66f7ba6d0ea340e1a769453e90da9d7d). The experiments were performed using PsychoPy software (v2022.2.4; Peirce et al., 2019), and participants completed the experiment in person.

Table 3.1 MDES questions.

Dimension	Questions	Scale Low	Scale High
Focus	My thoughts were focused on an external task or activity:	Not at all	Completely
Future	My thoughts involved future events:	Not at all	Completely
Past	My thoughts involved past events:	Not at all	Completely
Self	My thoughts involved myself:	Not at all	Completely
Other	My thoughts involved other people:	Not at all	Completely
Emotion	The emotion of my thoughts was:	Negative	Positive
Images	My thoughts involved images	Not at all	Completely
Detailed	My thoughts were detailed and specific:	Not at all	Completely
Deliberate	My thoughts were:	Spontaneous	Deliberate
Problem	I was thinking about solutions to problems (or goals):	Not at all	Completely
Intrusive	My thoughts were intrusive:	Not at all	Completely
Knowledge	My thoughts contained information I already knew (e.g., knowledge or memories):	Not at all	Completely
Absorption	I was absorbed in the contents of my thoughts	Not at all	Completely
Distracting	My thoughts were distracting me from what I am doing	Not at all	Completely
Words	My thoughts involved words	Not at all	Completely
Sounds	My thoughts involved sounds	Not at all	Completely

3.3.3. Procedure

During the experiment, text extracts were presented on the computer screen using PsychoPy, and the participants were asked to hit the spacebar every time they noticed their mind wandering (i.e. when they engaged in thought not directly related to the text they were reading). Each text was presented on a single screen. After reading each text, the MDES questions were presented followed by the three multiple-choice comprehension questions based on the text they had just read. Participants were allowed a short break before the next text. The experiment was self-paced and lasted around one hour. Participants completed both experiments in a counterbalanced order.

3.3.4. Analysis

Given distinct manipulations of difficulty for factual and story texts, analyses compare differences in mind-wandering or thought patterns across difficulty levels separately for each experiment, and then directly compare the two experiments.

Paired *t*-tests: mind-wandering frequency

The number of button presses during reading was used as an index of mind-wandering frequency. Prior to analysis, outliers in mind-wandering frequency were screened at the within-subject, within-condition level using a ± 2.5 SD criterion. No trials met this criterion; therefore, all analyses were conducted on the original data. For each participant, mind-wandering instances were averaged across trials within each difficulty condition separately for factual and story texts. When comparing the two text types, mind-wandering instances were likewise averaged across trials within each text type.

Within each experiment, the distribution of difference scores in mind-wandering frequency (easy vs. hard) was approximately symmetric, and paired *t*-tests were used to compare mind-wandering frequency between easy and hard conditions. The same approach was applied when comparing the two text types.

Principal component analysis: MDES

To identify common patterns of ongoing thoughts during text comprehension, we employed principal component analysis (PCA) on the responses to the 16 MDES questions

across all texts. Responses were standardized using z-scores before analysis. PCA with varimax rotation was performed in IBM SPSS Statistics (version 30), and parallel analysis implemented in R version 4.4.2 (R Core Team, 2024), was used to decide the number of components to interpret. Components with eigenvalues greater than 1 that were not retained by parallel analysis were included as covariates in subsequent models but were not interpreted further. Component loadings were visualised using word clouds generated in Python to aid interpretation; larger font size indicates stronger loadings, and colour denotes loading direction (red: positive; blue: negative).

Paired t-tests were used to assess differences in component scores between easy and hard texts separately for factual and story reading, as well as differences between text types. To control for multiple comparisons, p-values were Bonferroni-corrected within each set of tests based on the number of retained components.

Generalized linear mixed effects modelling: comprehension accuracy

To assess whether the patterns of ongoing thought during reading predicted comprehension accuracy, we employed generalized linear mixed models (GLMMs) using the `glmer` function in the `lme4` package in R version 4.4.2 (R Core Team, 2024). Comprehension accuracy for each text was modelled as a binomial response using the number of correct and incorrect responses with a logit link function. Following recommendations for mixed-effects modelling (Barr et al., 2013), we initially specified models with a maximal random-effects structure and then progressively simplified the random-effects terms to achieve convergence and avoid singular fits. Sum coding ($-0.5, 0.5$) was used for categorical variables. Post hoc comparisons were conducted using the *emmeans* package (Lenth, 2024).

To examine the relationship between thought patterns and comprehension accuracy across text types, we fitted a GLMM including fixed effects of five thought components, text types (factual, story), and their interactions. The final model included random intercepts for participants and items, as well as random slopes for one thought component by participant and by item, reflecting the most complex structure that converged reliably.

3.4. Results

3.4.1. Effect of difficulty on mind-wandering

Paired t-tests were conducted to examine differences in mind-wandering frequency between easy and hard texts separately for each experiment (see Figure 3.1). The results showed that, for both factual text and short story comprehension, mind-wandering frequency was significantly higher when participants read hard texts compared with easy texts (factual text: $t(91) = -7.49, p < .001$; short story: $t(91) = -3.51, p < .001$). When comparing the two text types, participants reported more mind-wandering during factual text comprehension than during short story comprehension ($t(91) = 5.79, p < .001$).

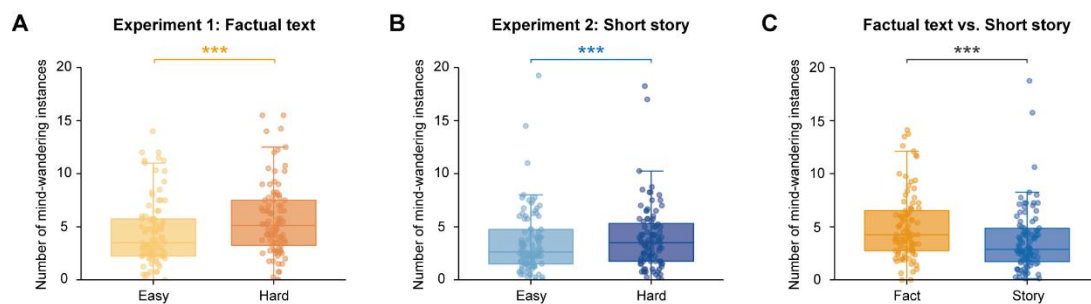


Figure 3.1 Mind wandering differences across text difficulty and text type. Boxplots show individual-level mind-wandering instances. Panel A shows the paired t-test results comparing easy and hard texts in factual texts. Panel B shows the same comparison within story texts. Panel C shows paired t-test results comparing factual texts and short stories. The box indicates the interquartile range (IQR), the horizontal line inside the box marks the median, and the whiskers extend to the most extreme data points within 1.5 times the IQR. *** $p < .001$.

3.4.2. PCA results: Patterns of ongoing thought

We performed PCA to decompose the MDES data to describe the pattern of ongoing thoughts reported by participants in different reading contexts. The PCA ($N = 92$) revealed five components with an eigenvalue > 1 , accounting for 56% of the total variance after varimax rotation (see Appendices, Figure S3.1A for scree plot). Parallel analysis indicated that the first four components were significant, and were therefore retained for interpretation

horizontal line inside the box marks the median, and the whiskers extend to the most extreme data points within 1.5 times the IQR. *** $p < .001$, ** $p < .01$, Bonferroni corrected.

The first component contributed 20% of the total variance, with high loadings for “future”, “problem”, “self” and “distracting”. This pattern of thought is referred to as “future problem solving” below. The second component (12% of the variance), labelled “intrusive social thought”, had high loadings on “sounds”, “intrusive”, “absorption” and “other”. Both patterns of thought showed negative loadings on “focus” suggesting that they occurred most often when people were not focussed on the reading task. The third component (9% of the variance), termed “knowledge retrieval”, loaded on “knowledge” and “past”; this thought pattern was near zero on the task focus question, suggesting it occurs both during text comprehension and when mind-wandering. The fourth component (8% of the variance), interpreted as “deliberate detail”, showed high positive loadings on “deliberate”, “detailed”, “emotion” (i.e. positive valence) items, and a negative loading on “distracting”. This component had a strong positive loading on “focus” showing that this pattern of thought occurred when people concentrated on the reading task.

3.4.3. Thoughts differences by difficulty and by text type

Paired t -tests were conducted to assess differences between texts in the patterns of thought that occurred (see Figure 3.2B and Figure 3.2C). A Bonferroni-corrected significance threshold of $\alpha = .0125$ was applied. For factual texts, hard texts had higher scores on Component 1, future problem solving ($t(91) = -3.87$, Bonferroni-corrected $p < .001$) and Component 2, intrusive social thought ($t(91) = -3.25$, Bonferroni-corrected $p = .007$), indicating that participants are more likely to generate these task-unrelated patterns of thought when reading factual texts that are challenging to understand. In contrast, participants showed higher scores on Component 4 indexing “deliberate detailed thought” when reading easy factual texts, with a trend toward significance after correction ($t(91) = 2.49$, Bonferroni-corrected $p = .058$). There was no significant difference between easy and hard texts for Component 3 ($t(91) = -.56$, Bonferroni-corrected $p = 1.0$).

For story text comprehension, replicating the pattern for expository texts, participants also showed more “deliberate detailed thought” (Component 4) when reading easy compared with hard story texts ($t(91) = 3.33$, Bonferroni-corrected $p = .005$). There was no difference between easy and hard texts for other thought components (Component 1: $t(91) = -2.17$, Bonferroni-corrected $p = .131$; Component 2: $t(91) = -2.22$, Bonferroni-corrected $p = .115$; Component 3: $t(91) = -.05$, Bonferroni-corrected $p = 1.000$).

We also examined differences in thought patterns between factual and story experiments (see Figure 3.2D). Participants were more likely to exhibit “future problem solving” (Component 1; $t(91) = 5.78$, Bonferroni-corrected $p < .001$) and “past knowledge” (Component 3; $t(91) = 4.65$, Bonferroni-corrected $p < .001$) when reading factual texts, and had higher scores on the “deliberate detailed” component (Component 4; $t(91) = -3.50$, Bonferroni-corrected $p = .003$) when reading story texts. There was no difference between factual text and stories for other components (Component 2: $t(91) = 1.12$, Bonferroni-corrected $p = 1.0$).

3.4.4. Thought patterns and comprehension accuracy

To examine whether patterns of ongoing thought during reading were associated with comprehension accuracy, we fitted GLMMs predicting accuracy from thought component scores. Comprehension accuracy was higher for stories than for factual texts (Table 3.2). Higher scores on the two task-unrelated components -- Component 1 (“future problem solving”) and Component 2 (“intrusive social thought”) -- were associated with poorer comprehension. In contrast, higher scores on Component 4 (“deliberate detail”) were associated with better comprehension.

Importantly, the strength of these relationships differed by text type. There was a significant interaction between text type and Component 1, indicating that although future-oriented problem solving was associated with poorer comprehension for both factual texts ($\beta = -.33$, $p < .001$) and stories ($\beta = -.15$, $p = .017$), this negative association was stronger for factual texts. A similar pattern was observed for Component 4: participants with higher scores for “deliberate detail” showed higher accuracy in both expository texts ($\beta = .31$, $p < .001$) and

story texts ($\beta = .14, p = .025$) but the positive impact of this thought pattern was larger for factual texts.

Table 3.2 Results of generalized linear mixed model predicting comprehension accuracy from thought components for all texts.

	β	SE	Z value	p
Intercept	1.20	0.17	7.06	< .001 ***
PC1	-0.24	0.04	-5.47	< .001 ***
PC2	-0.13	0.05	-2.30	0.021 *
PC3	0.07	0.04	1.53	0.127
PC4	0.22	0.04	5.02	< .001 ***
Task	0.66	0.32	2.09	0.037 *
PC1 $\times$ Task	0.18	0.08	2.23	0.026 *
PC2 $\times$ Task	0.04	0.09	0.44	0.662
PC3 $\times$ Task	-0.02	0.08	-0.30	0.762
PC4 $\times$ Task	-0.16	0.08	-2.04	0.041 *

3.5. Discussion

We conducted two experiments to examine how mind-wandering during reading varies as a function of text difficulty and text type, and how different patterns of ongoing thought relate to comprehension. Consistent with previous studies of reading (Laursen et al., 2024; Mills et al., 2017; Soemer et al., 2019), participants reported more mind-wandering when texts were more difficult, for both expository and narrative materials. This finding confirms that the relationship between task difficulty and mind-wandering is qualitatively different for reading than for many non-semantic tasks (McVay & Kane, 2009; Rummel & Boywitt, 2014; Smallwood & Schooler, 2015). Importantly, however, increased difficulty did not simply increase mind-wandering uniformly. Instead, difficulty altered the content of ongoing thought in different ways for factual and story texts, indicating that self-generated thought during reading is sensitive to the semantic context in which it occurs. Moreover, the relationship between ongoing thought and comprehension depended on text type, with

different patterns of internally generated thought hindering or supporting understanding in different reading contexts. Together, these findings suggest that mind-wandering during reading is content-sensitive rather than solely resource-limited, motivating a closer examination of (i) why difficulty increases mind-wandering during reading, (ii) how different forms of mind-wandering emerge under difficulty, and (iii) how the alignment between ongoing thought and semantic goals determines whether mind-wandering impairs or facilitates comprehension.

Why does difficulty increase mind-wandering during reading? One influential account proposes that mind-wandering reflects a failure of executive control: as task demands increase, control resources become insufficient to suppress task-unrelated thoughts, resulting in increased mind-wandering (McVay & Kane, 2010; McVay & Kane, 2012). This explanation is broadly consistent with our finding that difficult texts elicited more mind-wandering. However, it does not readily explain why reading and non-semantic tasks show a different relationship between difficulty and mind-wandering: in working memory and sustained attention paradigms, mind-wandering is typically more prevalent during relatively easy conditions, at odds with the predictions of this theory (Forster & Lavie, 2009; Konishi et al., 2017; Smallwood & Schooler, 2015).

One important difference between reading and non-semantic tasks is that successful reading depends on the retrieval and integration of semantic knowledge over time to construct a coherent situation model (Graesser et al., 1994; Smallwood, 2011; Zwaan & Radvansky, 1998). Semantic access is central to both text comprehension and internally generated thought (Binder et al., 2009; Smallwood, Bernhardt, et al., 2021; Smallwood & Schooler, 2015). As texts become more difficult, semantic processing becomes more effortful and the integration of incoming inputs is potentially less stable, increasing competition between externally driven comprehension and internally generated cognition. Within a predictive coding framework, semantic knowledge helps organise visual processing when texts are predictable, aligning bottom-up inputs with text-relevant semantic features (Clarke et al., 2013; Fabry & Kukkonen, 2019). When texts become difficult, however, this visual-semantic alignment is reduced, and in the absence of close visual coupling, semantic memory representations may

be harnessed by other patterns of thought that are independent of the text (Smallwood, Bernhardt, et al., 2021; Zhang et al., 2022; Zhang et al., 2019).

From this perspective, increased mind-wandering during difficult reading reflects competition for shared semantic resources, rather than executive failure alone. Consistent with this view, research in cognitive neuroscience has shown that increasing difficulty is associated with differential engagement of large-scale networks during semantic versus non-semantic tasks, including regions commonly described as part of the semantic control network in the left hemisphere and the bilateral multiple demand network (Davey et al., 2016; Jackson et al., 2016; Noonan et al., 2013). These studies suggest that difficulty may have qualitatively different consequences depending on whether it reflects the demands of semantic integration or non-semantic selection and inhibition. Overall, this semantic overlap account offers a parsimonious way to understand why increasing difficulty is associated with greater mind-wandering during reading, in contrast to many non-semantic tasks.

What different forms of thought occur during reading for stories and factual texts? A second implication of our findings is that mind-wandering during reading is heterogeneous rather than unitary. Increasing difficulty altered the composition of ongoing experience, giving rise to different patterns of thought in factual and narrative texts, consistent with the proposal that mind-wandering comprises multiple dimensions rather than a single state (Paul Seli et al., 2018; Smallwood & Schooler, 2015). Hard expository texts were associated with increased off-task thought, including internally generated future-oriented problem solving and thoughts about intrusive sounds (potentially reflecting environmental distraction). In contrast, hard-to-understand stories with an incoherent sentence order were primarily associated with a reduction in on-task, detailed, and deliberate thought accompanied by positive emotion and vivid imagery. In this way, our two contrasting difficulty manipulations did not affect mind-wandering in an identical fashion, even though mind-wandering frequency was found to increase in both cases.

This heterogeneity places important constraints on accounts of mind-wandering in reading. In particular, the executive failure hypothesis predicts a general decrease in task focus as control resources are taxed by difficult materials (Kane & McVay, 2012; McVay &

Kane, 2010), but does not readily explain why difficulty should lead to different kinds of thoughts in different hard reading contexts. Although the present study cannot determine whether these differences arise from the nature of the difficulty manipulation itself (e.g., greater semantic density and lexical–semantic precision versus disrupted narrative coherence), from broader genre-related expectations, or from an interaction between the two, the existence of multiple difficulty-sensitive thought patterns is theoretically informative. These findings support the view that mind-wandering during reading reflects competition within semantic systems that can give rise to qualitatively different experiential states, rather than a single failure mode of cognitive control (Andrews-Hanna, 2012; Binder et al., 2009; Murphy et al., 2019; Smallwood, Bernhardt, et al., 2021).

Beyond the effects of difficulty, there were also systematic differences between text types in the patterns of thought that emerged during reading. Factual texts elicited higher levels of future-oriented, task-unrelated thought, whereas story texts were associated with more deliberate, detailed, text-focused experiences. This pattern is consistent with the idea that narrative structure promotes a more immersive reading experience (Clinton et al., 2020; Mar et al., 2021), providing a potential explanation for the common observation that it can be difficult to remain engaged when reading factual materials such as textbooks, whereas mind-wandering during fiction reading may be less frequent or less disruptive. In addition, the knowledge retrieval dimension was largely neutral with respect to task focus and did not vary with difficulty, but was more prominent during factual text reading, consistent with greater engagement of prior knowledge during the processing of expository material (Best et al., 2008; Kendeou et al., 2016; McNamara & Magliano, 2009).

Which patterns of thought enhance and hinder comprehension during reading?

Finally, we found that different patterns of ongoing thought both helped and hindered comprehension, and that these functional effects were text-specific. Future-oriented problem solving was associated with poorer comprehension, while deliberate, detailed thought was linked to better comprehension. These findings align with prior work showing that mind-wandering can disrupt the flow of textual input and semantic processing, thereby impairing understanding (Smallwood, 2011; Zhang et al., 2022; Zhang et al., 2019). Importantly,

however, the impact of ongoing thought on comprehension depended on the type of text being read: off-task thought was more strongly related to comprehension of factual texts, consistent with a mind-wandering account, whereas the occurrence of positively valenced, deliberate, and detailed thought was more relevant for the comprehension of stories. Together, these findings indicate that the functional consequences of self-generated thought during reading reflect both the text and the content of thought in conjunction, consistent with a semantic overlap account.

We propose that mind-wandering during reading can be understood in terms of the *alignment* between ongoing thought and the semantic goals imposed by the text, rather than as a simple on-task versus off-task distinction. Internally generated thoughts that are misaligned with task demands -- such as future-oriented problem solving during factual reading -- are likely to compete with comprehension by interrupting the integration of incoming information. In contrast, text-focused, deliberate thought may support comprehension by stabilising and enriching semantic representations as they are constructed over time. Consistent with this view, mind-wandering has been shown to occur less frequently during story reading than during factual reading, suggesting a more immersive reading experience for narratives (Clinton et al., 2020; Mar et al., 2021).

Crucially, the ease with which semantic alignment can be maintained appears to differ across text types. Narrative texts provide a coherent temporal and causal structure that may scaffold internally generated thought, allowing readers to remain engaged even when attention drifts from surface-level input. In contrast, factual texts place greater demands on precise semantic access and controlled integration of information (Aboud et al., 2019; Eason et al., 2012), and lack a narrative framework to support the incorporation of self-generated thought. As a result, comprehension of factual texts may be more vulnerable to the occurrence of off-task thoughts.

Conclusion: Our findings show that reading is accompanied by multiple patterns of thought that vary as a function of both text difficulty and text type, with distinct consequences for comprehension. Some forms of internally generated thought, such as future-oriented or intrusive thinking, are more prevalent during difficult reading and are associated with

impaired understanding, particularly for factual texts. In contrast, deliberate and detailed thought that remains aligned with the content of the text supports comprehension, especially during narrative reading. Together, these findings suggest that the functional impact of mind-wandering during reading depends on the alignment between ongoing thought and the semantic goals imposed by the text, rather than on task engagement alone.

Chapter 4. Retinotopic coding predicts individual differences in sustained focus during comprehension and recall

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4.1. Abstract

Deactivation during task-based fMRI is often interpreted as reflecting perceptual decoupling or task disengagement. Yet recent work challenges this view by showing that negative retinotopic mapping embedded in higher-order cortex potentially supports scene construction and memory retrieval. We combined retinotopic mapping with comprehension and autobiographical memory recall tasks in the same participants, to examine how retinotopic coding constrains focus across cognitive modes. Retinotopic coding was distributed across the cortex, with the strongest positive effects in visual and dorsal attention networks, while other networks showed similar levels of positive and negative retinotopic coding. Principal component analysis revealed three principal patterns of retinotopic organisation, which showed distinct associations with the relationship between neural activity and task focus during externally and internally oriented cognition. Stronger positive retinotopic coding within default mode regions was associated with greater suppression of frontal control areas during focused comprehension and increased occipital engagement during autobiographical recall. In contrast, positive retinotopic coding within attentional control networks was linked to externally oriented focus during auditory comprehension but reduced engagement of medial temporal and anterior temporal regions during autobiographical memory recall. Negative retinotopic coding in heteromodal networks was associated with efficient suppression of off-task regions when visual input was irrelevant, but increased recruitment of frontal control regions when visual information was task-relevant. These findings suggest that retinotopy structures the integration and suppression of perceptual information, modulating the contribution of semantic, memory, and executive control processes to task focus.

4.2. Introduction

Task-based fMRI consistently reveals widespread activation in sensory, attention, and control networks alongside deactivation in default-mode (DMN) and limbic regions (Fox et al., 2005; Menon, 2023; Raichle et al., 2001). While this has typically been interpreted as a functional antagonism, supporting task focus versus disengagement, recent evidence suggests

that deactivation is not equivalent to a lack of engagement, as functional connectivity can increase even during DMN deactivation and may be accompanied by high decoding accuracy (Krieger-Redwood et al., 2016; Wang et al., 2021). Shao et al. (2024) found that some task manipulations of the difficulty of semantic processing increase both activation and deactivation at the same time and within the same network. In addition, Leech et al. (2025) demonstrated that the spatial distribution of BOLD deactivation can be predicted from the layout of activation, and vice versa, across tasks, individuals, and even species. Using a geostatistical interpolation method (kriging), they showed that antagonistic patterns (increases and decreases) are topographically structured across the cortex – not random opposites but spatially mirrored patterns. This implies that the architecture governing BOLD deactivation is intimately tied to the geometry of activation, raising the question: what spatial principles underlie this precise arrangement?

Retinotopic mapping is a defining feature of the early visual cortex, but accumulating evidence indicates that spatial representations of the visual field persist far beyond occipital areas (Angeli et al., 2024; Groen et al., 2022; Knapen, 2021). Visual field maps have been identified in dorsal attention and frontoparietal control networks, consistent with their role in spatial attention and eye movement planning (Mackey et al., 2017; Silver et al., 2005; Vossel et al., 2014). More unexpectedly, retinotopic structure has also been observed in regions traditionally considered transmodal, including parts of the default mode network (DMN; Knapen, 2021; Steel et al., 2025; Steel et al., 2024; Szinte & Knapen, 2020). Notably, Steel et al. (2024) have shown that medial parietal and ventral DMN regions exhibit negative population receptive fields (pRFs), where neural populations respond more strongly to regions of the visual field that are *not* currently stimulated. This signature is associated with memory-guided, internally directed visual processing (Steel et al., 2024). These findings challenge the conventional view that transmodal cortex is agnostic to visual space, and instead suggest that representations of visual field position remain embedded in heteromodal regions, potentially supporting visual scene construction and memory retrieval (Groen et al., 2022; Steel et al., 2024).

Given that negative retinotopic coding has been proposed to reflect active disengagement from perceptual input or the prioritisation of internally generated representations, this raises the possibility that retinotopic organisation in transmodal cortex does not simply represent visual space, but regulates when perceptual information is integrated or suppressed, thereby shaping the balance between externally oriented attention, semantic processing, and internally generated cognition. In this way, individual differences in positive and negative retinotopic signals may alter attentional focus depending on both current goals and input modality. However, the functional relevance of retinotopic organisation for task focus has remained largely unexplored. In this study, we address this gap by examining how large-scale patterns of retinotopic organisation, captured via principal component analysis (PCA), relate to participants' ability to sustain focus during both externally oriented tasks (e.g., reading) and internally oriented tasks (e.g., autobiographical memory retrieval). By linking individual differences in sustained task focus to the spatial structure of retinotopy across cortex, we test the hypothesis that the embedding of visual field representations in high-level cortex constrains how attentional focus is implemented across cognitive modes, rather than simply whether attention is directed outwards or inwards.

4.3. Methods

4.3.1. Participants

We recruited 30 participants (24 females, 6 males, mean age = 20 years, range = 18-23 years). All were right-handed native English speakers, and had normal or corrected-to-normal vision, (except one with amblyopia in the right eye was excluded from retinotopy analysis). Therefore, the final sample of retinotopy analysis included 29 participants (23 females, 6 males, mean age = 20 years, range = 18-23 years).

The same sample of participants conducted comprehension and recall tasks in fMRI (4 participants excluded due to insufficient data to model the parametric effect of task focus; see Study 2 in Chapter 2). Therefore, 25 participants were included in the analysis that related retinotopy with focus effect of comprehension and recall (19 females, 6 males, mean age = 20 years, range = 18-23 years).

None of the participants had any history of neurological impairment, diagnosis of learning difficulty or psychiatric illness. All provided written informed consent prior to taking part. Participants were recruited through participant pools, and paid for their time or awarded course credits. Ethical approval was obtained from the Research Ethics Committees of the Department of Psychology and York Neuroimaging Centre, University of York (Project number: P1406).

4.3.2. Task materials and procedures

Retinotopy task

The retinotopic stimulus followed the design of bar stimuli used elsewhere (Lowndes et al., 2023; Welbourne et al., 2018). A bar with a width of 1.25 degrees moved within a 20 degrees diameter circular aperture, stepping once per TR (1500 ms) across 16 positions for each direction. The bar pattern reversed contrast at 2 Hz. Eight directions were presented, including four cardinal directions and four diagonal directions (see Figure 4.1A). Four 12-second blank periods occurred during the second half of the four diagonal directions. Participants performed a button press when the fixation cross changed colour as an attentional task to aid fixation. Four scan repeats were carried out for each participant. The scan session for the retinotopy lasted for approximately 12.8 min and comprised four runs.

comprehension task, participants read or listened to factual sentences. In the recall task, participants recalled personal memories while ignoring visual or auditory sentences, or without distraction. At the end of each trial, participants rated their level of focus on a scale of 1 to 4.

Comprehension and recall tasks

This study occurred across two consecutive days (more details see Study 2 in Chapter 2). On day 1, participants generated their personal memories associated with autobiographical cue words (e.g., gift) outside the scanner. They were asked to identify specific personal events and to provide as much detail as they could (e.g., time, location, who was involved, what happened, and the duration), which were entered into a spreadsheet to ensure that comparable information was recorded for different cue words.

On day 2, in the scanner, participants engaged in recalling their personal memories or performing a comprehension task (see Figure 4.1B). Each trial started with a fixation cross (1-3 s) in the centre of the screen, followed by a 2 s written and spoken autobiographical memory cue word, during which participants recall their associated personal memories. Next, the task instruction (i.e., COMPREHEND or RECALL) was presented visually or auditorily for 1 s, followed by main trial stimuli lasting for 7.8-10.2 s (average 9 s). Stimuli consisted of either sentences (visual or auditory) or matched control stimuli (series of x or white noise). The visual sentences were presented on 13-17 successive slides, with each one lasting 600 ms, combining short words or articles and conjunctions together with nouns. The auditory sentences were presented naturalistically, with the sentence unfolding as the speaker intended. The visual instructions and sentences were presented together with white noise, and the auditory ones were paired with varying-length letter strings (e.g., XXXXX; XXX, etc.), ensuring sensory inputs were presented in both visual and auditory channels across conditions. On memory recall trials without a conflicting sentence, task instructions were presented visually on half the trials and auditorily on the other half, followed by both letter strings and white noise. On memory recall trials, participants were instructed to keep thinking about their autobiographical memory in detail until the end of the trial. Each trial was

followed by a jittered fixation (1-3 s) and a task focus rating, where participants rated their task focus on a scale of 1 (i.e., not at all focused) to 4 (i.e., highly focused) within 2 s, using a button press.

4.3.3. fMRI data acquisition

Whole brain structural and functional MRI data were acquired using a 3T Siemens MRI scanner utilising a 64-channel head coil, tuned to 123 MHz at the York Neuroimaging Centre, University of York. We used a multiband-multiecho (MBME) EPI sequence with the following parameters: TR=1.5 s; TEs = 12, 24.83, 37.66 ms; 48 interleaved slices per volume with slice thickness of 3 mm (no slice gap); FoV = 24 cm (resolution matrix = 3x3x3; 80x80); 75° flip angle; volumes per run below; 7/8 partial Fourier encoding and GRAPPA (acceleration factor = 3, 36 ref. lines; multi-band acceleration factor = 2).

Structural T1-weighted images were acquired using an MPRAGE sequence (TR = 2.3 s, TE = 2.26 s; voxel size = 1x1x1 isotropic; 176 slices; flip angle = 8°; FoV= 256 mm; interleaved slice ordering).

The retinotopy task was presented across four runs, each lasting 3.2 min, with 128 volumes in each run. The comprehension and recall task presented across four runs, each lasting 9.35 min, with 374 volumes in each run.

4.3.4. fMRI data analysis

Preprocessing

Retinotopy task: Anatomical images segments were generated using `fsl_anat` (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/fsl_anat; brain extraction (using FNIRT, BET)) and aligned to the fMRI data using FLIRT. Anatomical images surfaces were generated using FreeSurfer 7.3.2 (Fischl, 2012) and aligned to the fMRI data using `@SUMA_AlignToExperiment`.

The multi-echo data were pre-processed using AFNI (<https://afni.nimh.nih.gov/>), including de-spiking (3dDespike), slice timing correction (3dTshift), and motion correction (3dvolreg applied to echo 2 to realign all images to the first volume; these transformation parameters were then applied to all runs). Tedana (TE Dependent ANALysis; version v23.0.1;

DuPre et al., 2021; Kundu et al., 2013; Kundu et al., 2012; The tedana Community et al., 2023) was used to combine the three echoes. The optimally combined, denoised signals were averaged across runs and normalized to percent signal change.

Comprehension and recall tasks: The multi-echo data preprocessing followed a similar pipeline to that used for the retinotopy task, and tedana was used for multi-echo images combination (see Chapter 2 for details). Denoised optimally-combined time series data were pre-processed using FSL, including high-pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with $\sigma = 100s$), linear co-registration to the corresponding T1-weighted image and to MNI152 standard space (Jenkinson & Smith, 2001), spatial smoothing using a Gaussian kernel with full-width-half-maximum (FWHM) of 6 mm, and grand-mean intensity normalisation of the entire 4D dataset by a single multiplicative factor.

Population Receptive Field (pRF) Modelling

We ran the pRF model using a non-linear fitting algorithm in AFNI (3dNLFit; as described in Silson et al., 2015; Steel et al., 2024). The best explained pRF parameters for each voxel were selected by simultaneously using both Simplex and Powell optimization algorithms to minimize the least-squares error between the acquired retinotopy time series and the amplitude-scaled prediction. The estimated pRF parameters included the pRF position (x, y), size (σ), amplitude (positive, negative). The pRF amplitude reflects the relative activation or deactivation to visual stimulation of its receptive field. Important for the current study, PRF coefficient of determination (R^2) multiplied by the sign (positive or negative) of the estimated amplitude parameter, reflected the quality of the model fit for both positive and negative pRFs.

For current study, pRFs R^2 were visualized on the cortical surface using SUMA software (Saad & Reynolds, 2012), as a function of the sign of the best explained amplitude parameters (see Figure 4.2A for the retinotopic map from averaged time series across participants).

Comprehension and recall tasks fMRI data analysis

Pre-processed time series data were modelled using a general linear model correcting for local autocorrelation (Woolrich et al., 2001). Ten Explanatory Variables (EV) of interest and four of no interest were modelled using a double-Gaussian hemodynamic response gamma function. The ten EVs of interest were as follows: (1) visual comprehension; (2) auditory comprehension; (3) recall while ignoring visual sentences; (4) recall while ignoring auditory sentences; (5) recall without distraction; (6-10) task focus effects for each of the five experimental conditions as parametric regressors. EVs of no interest were: (11) memory cue word, (12) task instruction, (13) fixation (the period before the rating question) and (14) rating decision period. No motion parameters were included due to prior denoising with the tedana pipeline (Kundu et al., 2012). EVs for each condition commenced at the onset of the first word or letter string, with duration set as the stimulus presentation time. The parametric EVs for task focus shared the same onset and duration as their respective trials, weighted by demeaned task focus ratings. Runs with no variability in task focus rating within a condition were excluded, resulting in the removal of four participants; on average, over 77% of the data was retained. The fixation period between trials provided the implicit baseline. In the group-level analysis, clusters were corrected using a threshold of $Z = 3.1$ to define contiguous clusters (Worsley, 2001) and a familywise-error-corrected (FWE) significance level of $p < .05$.

Similarities between distribution of pRFs R^2 map and principal gradient

To examine whether the distribution of positive- and negative-amplitude pRFs is correlated with the principal gradient of cortical organization, we used spin permutation tests to assess the spatial correlation between the retinotopic R^2 maps and the principal gradient defined by Margulies et al. (2016). 5000 permutations of randomly rotated data were generated for the principal gradient map while preserving the spatial autocorrelation, and permutation correlation values were then compared with the null distribution to assess statistical significance. To focus on the gradient from visual cortex to heteromodal networks, we excluded the motor regions defined in Schaefer 7 network atlas (Schaefer et al., 2018) in the analysis (see Appendices, Figure S4.1 for spin test results of whole brain maps).

Linear mixed-effect modelling: exploring the distribution of pRFs R^2

To examine how positive and negative pRFs are distributed across whole-brain networks, we employed the Schaefer 400 parcel, 7 network atlas (Schaefer et al., 2018) to assess the distribution pattern of pRFs. Before the analysis, we removed 1% of the pRFs R^2 that fell outside the mean ± 3 standard deviations (SD) for each parcel.

We used linear mixed-effects in R version 4.4.2 (R Core Team, 2024) to estimate the effects of the network, hemisphere and pRFs on R^2 values. We first employed a model including the fixed effects of network (visual, somatomotor, dorsal attention (DAN), ventral attention (VAN), control, default, and limbic networks), hemisphere (left, right) and pRFs (positive, negative), and their interactions, with adjustments for random intercepts for participants and parcels, as well as by-participant and by-parcel random slopes for hemisphere and pRFs. The dependent variable was the R^2 value associated with each combination of network, hemisphere and pRFs.

To further investigate pairwise differences between networks, we conducted nine linear mixed-effects models, each comparing two networks at a time. Each model included fixed effects of networks, pRFs, and their interaction, with adjustments for random intercepts for participants and parcels, as well as by-participant and by-parcel random slopes for pRFs. The dependent variable was R^2 value associated with each combination of network, hemisphere and pRFs. *P*-values were Bonferroni-corrected to control multiple comparisons.

All models were initially the full model, including all random factors (Barr et al., 2013). The random effect structure was simplified stepwise until the model successfully converged and no singular fitting warning was reported. The significance testing for the fixed effects was conducted using the lmerTest package (Kuznetsova et al., 2017). The emmeans package (Lenth, 2024) was used to make post hoc comparisons. The scripts and the complete lists of fixed and random effects are presented in OSF (https://osf.io/95xym/overview?view_only=0761c1182c3b4562b6eb95c37b68847f).

Principal Component Analysis

To better understand the underlying structure of positive and negative pRFs across whole-brain regions, we employed the principal component analysis (PCA) on the matrix comprising R^2 for positive and negative pRFs. Given the variability observed between

subnetworks within the seven networks (see Appendices, Table S4.4), we extracted the R^2 of the 17 functional networks defined by the Schaefer 400 parcels, 17 network atlas (Schaefer et al., 2018). The PCA was performed with varimax rotation in IBM SPSS Statistics (version 30), and the parallel analysis was conducted in R version 4.4.2 (R Core Team, 2024). All data were standardized before PCA analysis. Word clouds representing loadings for each component were generated to visualize using Python. The larger font size indicates greater loading of the item on the dimension and the colour represents the direction of this loading (red: positive; blue: negative).

Neural association between pRFs and focus effects

The PCA scores were entered as regressors in the group level ($N = 25$) general linear modal (GLM) analysis in comprehension and recall study. The design matrix consisted of a constant term representing the focus effects across all five conditions, along with additional columns corresponding to the PCA component scores for each condition. Group level maps were thresholded with a FWE threshold of $p < 0.05$ and a z -statistic threshold of 2.6. By using association maps as masks, focus effect maps were visualized with group-level z -statistic threshold of 1.96 (positive: dark red; negative: dark blue) and 2.6 (positive: bright yellow; negative: bright blue).

4.4. Results

4.4.1. Whole-brain distribution of positive and negative pRFs

Our first analysis examined the distribution of positive and negative retinotopic maps across the cortex. We examined the cortical distribution of positive- and negative-amplitude population receptive fields (pRFs) by multiplying the coefficient of determination (R^2) by the sign of the best-fitting amplitude parameter. This approach allowed us to represent both the strength of retinotopic tuning and the direction of the BOLD response within a single map.

The group averaged whole-brain R^2 map ($N = 29$) is shown in Figure 4.2A. Positive amplitude pRFs (+pRFs) are represented with warm colours, while negative amplitude pRFs (−pRFs) are represented with cold colours. As expected, we observed robust retinotopic coding in visual areas (Wandell et al., 2007). Beyond these regions, lower amplitude +pRFs were observed across parietal, frontal, and temporal cortex. There were also −pRFs, reflecting

negative BOLD responses to visual stimulation, across occipital, parietal, temporal and frontal regions. Taken together, these results reveal that large-scale visual organization comprises both positive- and negative-amplitude retinotopic responses distributed across the cortex.

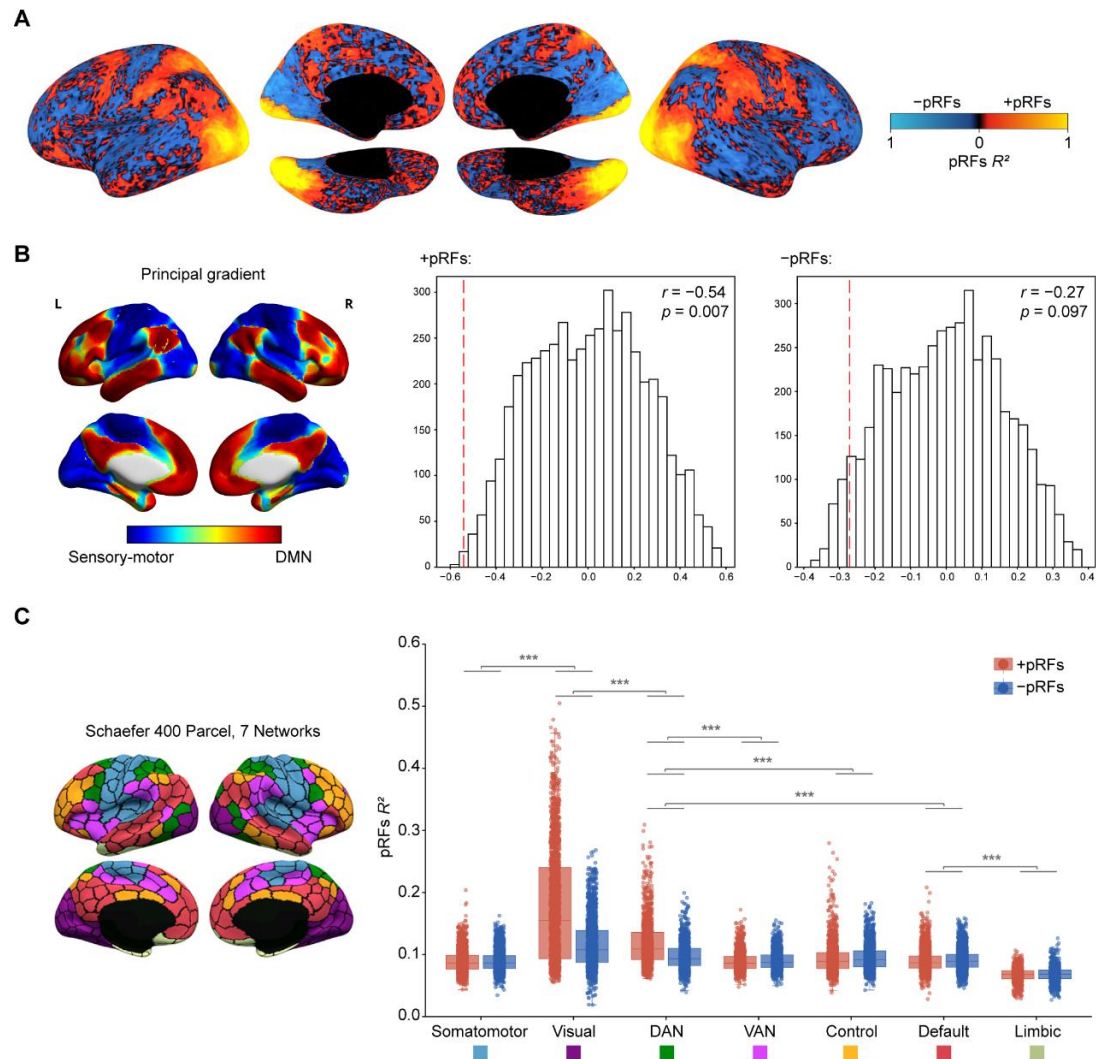


Figure 4.2 Positive and negative pRFs throughout the cortex. (A) Inflated lateral, ventral, and medial views depict the coefficient of determination of the pRF model prediction ($pRF R^2$) multiplied by the sign of the estimated amplitude parameter (colour scale: +pRFs: red colours; -pRFs: blue colours), for the averaged time series across the participants. (B) Statistical significance of correlations between positive/negative retinotopic coding maps and the principal gradient was assessed using the spin permutation test (5000 permutations). The left

map presents the principal gradient from Margulies et al. (2016). (C) The boxplots show the individual parcel-level R^2 of positive and negative pRFs in networks defined in Schaefer et al. (2018). The colours represent the type of pRFs (warm: +pRFs; cold: -pRFs). The box indicates the interquartile range (IQR), the horizontal line inside the box marks the median, and the whiskers extend to the most extreme data points within 1.5 times the IQR. Statistical comparisons are based on the linear mixed-effects models (see Appendices, Table S4.1). The left map presents the 400 parcel parcellation matched to Yeo 7 network parcellation from Schaefer et al. (2018). *** $p < .001$.

Next, we asked whether the spatial distribution of +pRFs and -pRFs is structured according to the unimodal-transmodal axis described by Margulies et al. (2016). We conducted spin permutation tests with 5000 permutations to assess spatial correlations with positive- and negative-amplitude pRFs and the principal gradient excluding motor regions (results of permutation tests with the whole principal gradient are provided in Appendices, Supplementary Materials). The distribution of +pRFs was significantly negatively correlated with the principal gradient ($r = -.54$, $p_{\text{spin}} = .007$; Figure 4.2), suggesting that regions with stronger R^2 for +pRFs tend to align with the visual end of the gradient. In contrast, no correlation was found for -pRFs ($r = -.27$, $p_{\text{spin}} = .097$). These results suggest that positive-amplitude retinotopic coding follows the brain's dominant axis of cortical organisation, whereas negative-amplitude retinotopic responses are not similarly constrained.

4.4.2. Network analyses

To better characterise the large-scale topography of visual coding beyond early visual cortex, we next examined how retinotopic tuning strength varied across canonical functional networks. We used the Schaefer 400 parcels for 7 networks as regions of interest and quantified the distribution of R^2 values for positive- and negative-amplitude pRFs within each network ($N = 29$).

First, we asked whether retinotopic tuning strength differs systematically across networks and between pRF types. We conducted a linear mixed-effects model including

network and pRF type as fixed effects. There was a significant main effect of network ($F(6,385) = 66.885, p < .001$) and pRFs type ($F(1,66) = 25.225, p < .001$), and an interaction between network and pRF type ($F(6,386) = 55.379, p < .001$), showing that differences in the tuning strength of +pRFs and -pRFs vary across networks. To interpret this interaction, we conducted post hoc pairwise comparisons of +pRFs and -pRFs within each network using estimated marginal means with Bonferroni correction. Significant differences were found in the visual network ($Z = 17.061, p < .001$) and dorsal attention network ($Z = 5.199, p < .001$), where R^2 values were higher for +pRFs than -pRFs. No significant differences were observed in the other networks after correction (Appendices, Table S4.1 and Table S4.2).

We next asked whether differences in retinotopic tuning strength follow the hierarchical ordering of networks along the principal cortical gradient. To test this, we performed pairwise linear mixed-effects models comparing networks that are adjacent along the principal gradient (Appendices, Table S4.3 provides main effects and interaction effects for each network pair). The visual network had higher R^2 than somatomotor and dorsal attention networks for both +pRFs and -pRFs, and a stronger bias towards +pRFs. Dorsal attention network had higher R^2 for both +pRFs and -pRFs compared with ventral attention and default networks, and again a stronger bias towards +pRFs. Dorsal attention also showed significantly higher R^2 than control network regions for +pRFs but not -pRFs. There were no differences in pRFs between ventral attention, control and default mode network in either the magnitude or direction of pRFs. However, the default network showed higher R^2 than the limbic network., with differences for both +pRFs and -pRFs.

Finally, to assess heterogeneity within networks, we repeated the linear mixed-effects analyses at the subnetwork level by mapping the Schaefer 17-network parcellation onto the corresponding 7-network atlas (See Appendices, Figure S4.2 , Table S4.4). Within both the visual network and dorsal attention network, most subnetworks showed higher R^2 for +pRFs, although effect sizes varied significantly across subnetworks. In contrast, within the limbic network, limbic subnetwork B showed higher R^2 for -pRFs than +pRFs, whereas no such difference was observed in limbic subnetwork A, indicating heterogeneous pRFs distributions within the limbic network.

4.4.3. PCA analysis results

The results so far reveal a high degree of variability in retinotopic tuning between and within large-scale networks. To characterise the dominant patterns underlying this variability, we performed PCA ($N = 29$). This analysis was applied to positive- and negative-amplitude R^2 values across the Schaefer 17-network parcellation (Schaefer et al., 2018). Six components were identified based on the scree plot, explaining $>84\%$ of the variance after varimax rotation; parallel analysis indicated that the first three components were robust and together explained 71% of the variance (Appendices, Figure S4.3). These were taken forward for interpretation, with remaining components included as covariates.

The first three components (Figure 4.3) captured distinct large-scale patterns of retinotopic organisation. Component 1 reflected negative retinotopic responses in heteromodal control and attention networks. Component 2 was characterised by positive retinotopic responses in control and attention networks. Component 3 captured positive retinotopic responses in default mode and frontal limbic networks.

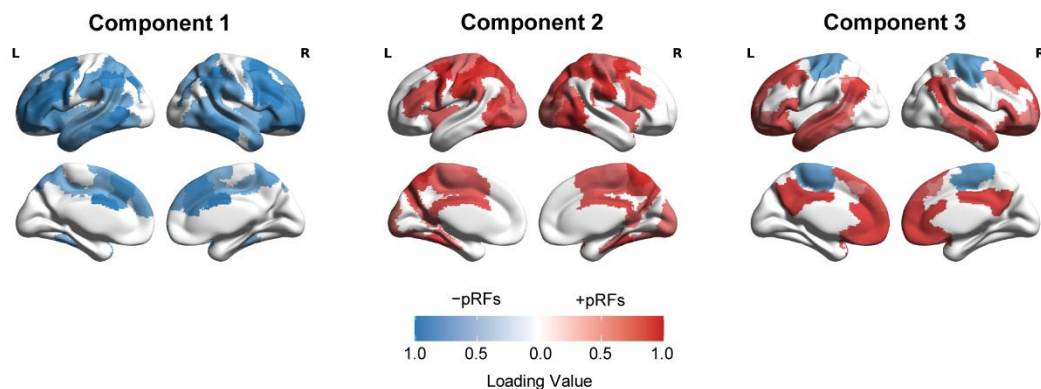


Figure 4.3 PCA loadings for the first three principal components identified in our analysis. PCA component loadings were visualized on the cortical surface, with colours indicating positive and negative pRFs loadings (+pRFs: red; -pRFs: blue). A threshold of 0.55 was applied to ensure that the +pRFs and -pRFs did not overlap.

4.4.4. Neural correlation of PCA components

We next asked whether these large-scale retinotopic patterns related to neural focus effects during reading comprehension and autobiographical memory retrieval. Group-level GLMs tested whether PCA component scores linked to positive and negative retinotopy across networks could predict focus-related activity ($N = 25$).

Component 3 (default/limbic +pRFs) showed the clearest relationship with focus. During both auditory and visual comprehension, higher component scores were associated with more negative focus-related activation in medial and lateral frontal regions, particularly anterior cingulate, paracingulate cortex and middle frontal gyrus (Figure 4.4A) that deactivated in response to higher levels of task focus (Figure 4.4B). This effect was modality-invariant and confirmed by conjunction analysis across visual and auditory comprehension (Figure 4.4C). Therefore, during focussed comprehension, individuals with stronger visual coupling to DMN showed better suppression of regions that were negatively associated with focus. These findings might reflect the way that visual inputs can penetrate semantic DMN regions to support the task, regardless of the input modality.

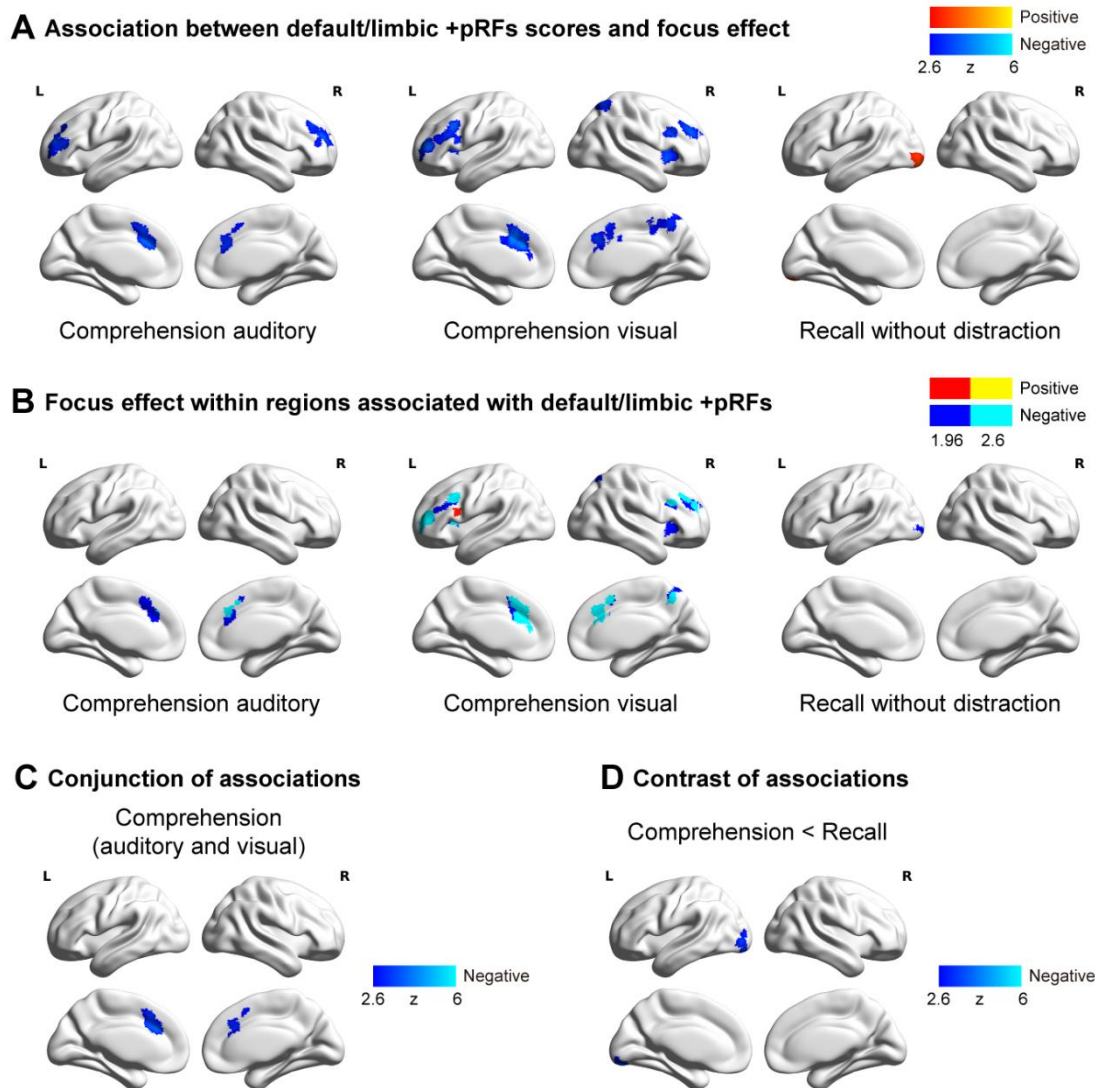


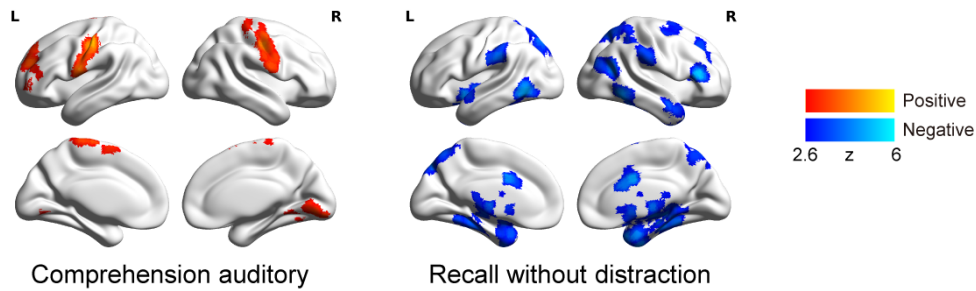
Figure 4.4 Relationship between PCA component 3 (default/limbic +pRFs) and focus-related brain activation. (A) Brain maps showing regions in which focus effect was significantly associated with component 3 (default/limbic +pRFs). Participants with higher scores showed greater (red) or weaker (blue) focus effect, during either comprehension or memory retrieval tasks. (B) Focus effect maps masked by association maps in (A). Warm colours (red/yellow) indicate greater activation with increasing focus, whereas cool colours (blue) indicate greater deactivation. For visualization, maps are shown at $z > 1.96$ (dark red/blue) and $z > 2.6$ (bright yellow/blue). (C) Formal conjunction of associations between component 3 and focus effect from auditory and visual comprehension in (A), conducted using FSL “easythresh_conj” tool. These regions showed reduced (blue) focus effect with increasing PCA component 3 scores

during comprehension. (D) A comparison of associations between component 3 and focus effect during comprehension and memory retrieval tasks. Blue regions indicated stronger association effects during memory retrieval task.

During autobiographical memory retrieval without distraction, the same PCA component showed a positive association with focus effects in occipital cortex (Figure 4.4D), consistent with increased engagement of visual regions during vivid internally generated memory. Together, these findings suggest that stronger visual coupling within default mode systems may contribute to sustained focus by suppressing task-irrelevant control regions during comprehension, while enhancing visual imagery during recall.

Component 2 (control/attention +pRFs) showed a different pattern. During auditory comprehension, higher scores were associated with increased focus-related activation in sensorimotor, visual and frontal regions (Figure 4.5A; Figure 4.5B). In contrast, during autobiographical memory retrieval without distraction, higher scores were associated with reduced activation across medial temporal, parietal and anterior temporal regions, including regions that typically show increased activation with better memory focus. This pattern suggests that strong visual coupling within control systems may support externally oriented focus during auditory comprehension yet interfere with internally generated memory, necessitating the suppression of mnemonic regions that are positively associated with focus during recall (Figure 4.5B).

A Association between control/attention +pRFs scores and focus effect



B Focus effect within regions associated with control/attention +pRFs

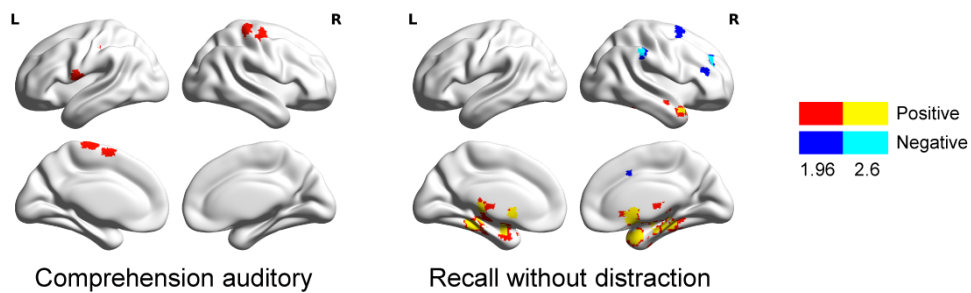
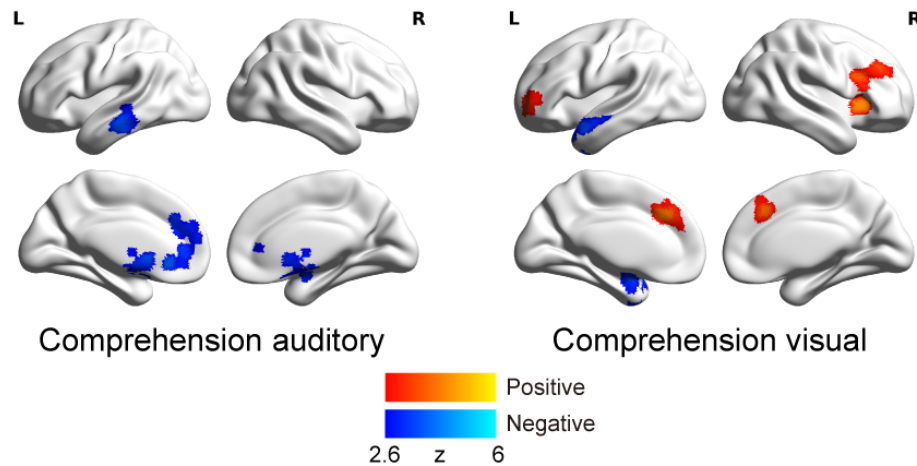


Figure 4.5 Relationship between PCA component 2 (control/attention +pRFs) and focus-related brain activation. (A) Brain maps showing regions in which focus effect was significantly associated component 2 (control/attention +pRFs). Participants with higher scores showed greater (red) or weaker (blue) focus effect, during either auditory comprehension or memory retrieval tasks. (B) Focus effect maps masked by association maps in (A). Warm colours (red/yellow) indicate greater activation with increasing focus, whereas cool colours (blue) indicate greater deactivation. For visualization, maps are shown at $z > 1.96$ (dark red/blue) and $z > 2.6$ (bright yellow/blue).

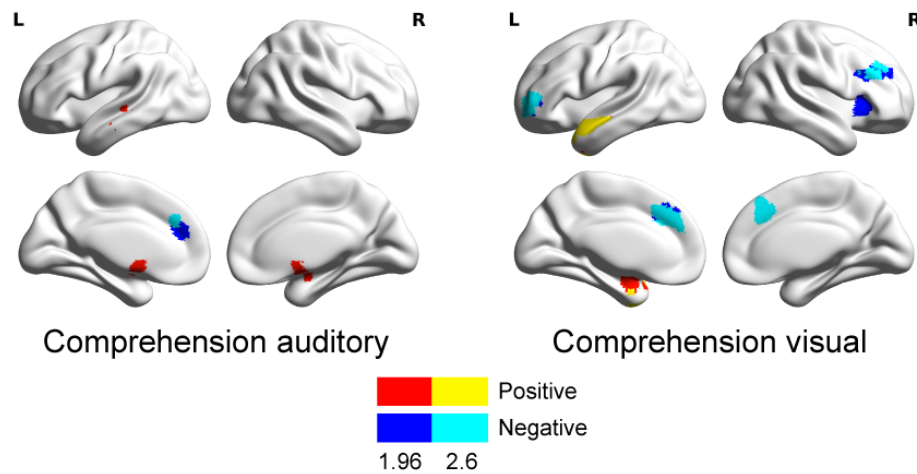
Component 1 (heteromodal –pRFs) showed marked modality-dependent effects on comprehension-related focus. During auditory comprehension, higher scores on this component were associated with greater suppression of activity in medial prefrontal regions associated with low task focus, consistent with efficient filtering of task-irrelevant visual input. Reduced activation was also observed in lateral temporal regions not associated with off-task states.

In contrast, during visual comprehension, the same retinotopy component was associated with increased activation in dorsomedial prefrontal cortex, frontal pole and right dorsolateral prefrontal cortex – regions negatively associated with task focus (Figure 4.6). This pattern was accompanied by reduced activation in anterior temporal regions that showed positive associations with focus during auditory comprehension. Direct contrasts confirmed that the relationship between Component 1 and focus was stronger during visual than auditory comprehension (Figure 4.6C). This pattern suggests that widespread negative retinotopic coding in heteromodal networks is associated with greater deactivation of off-task medial prefrontal regions when visual input is irrelevant, but activation of control regions when visual information is task-relevant.

A Association between heteromodal –pRFs scores and focus effect



B Focus effect within regions associated with heteromodal –pRFs



C Contrast of associations

Comprehension Auditory < Visual

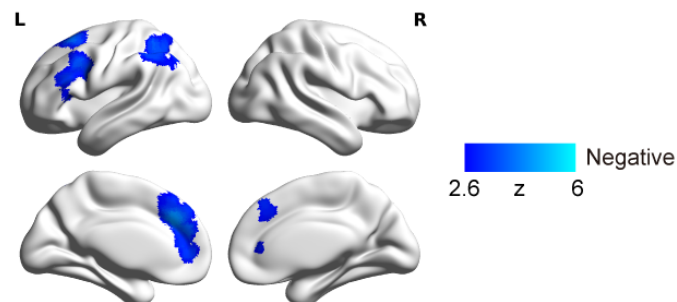


Figure 4.6 Relationship between PCA component 1 (heteromodal –pRFs) and focus-related brain activation. (A) Brain maps showing regions in which focus effect was significantly associated with component 1 (heteromodal –pRFs). Participants with higher scores showed greater (red) or weaker (blue) focus effect, during either comprehension or memory retrieval

tasks. (B) Focus effect maps masked by association maps in (A). Warm colours (red/yellow) indicate greater activation with increasing focus, whereas cool colours (blue) indicate greater deactivation. For visualization, maps are shown at $z > 1.96$ (dark red/blue) and $z > 2.6$ (bright yellow/blue). (C) A comparison of associations between component 1 and focus effect during auditory and visual comprehension. Blue regions indicated stronger association effects during visual comprehension.

4.5. Discussion

To examine the functional role of retinotopic coding beyond early visual cortex, we combined retinotopic mapping with comprehension and autobiographical recall tasks in the same participants. Retinotopic coding was distributed across the cortex, with the strongest effects in visual and dorsal attention networks, especially for positive retinotopic signals; in other networks, there was a similar distribution of positive and negative retinotopic coding. Dimensionality reduction using PCA revealed three principal patterns of retinotopic organisation, which were associated with distinct relationships between neural activity and task focus during externally and internally oriented cognition in distinct ways. Overall, the findings suggest that retinotopic coding might provide a systems-level mechanism that can regulate focus by shaping how perceptual information is integrated or suppressed across large-scale networks.

Earlier research showed retinotopic coding within heteromodal regions of DMN (Steel et al., 2025; Steel et al., 2024; Szinte & Knapen, 2020), with negative retinotopic coding within medial temporal memory regions in functional opposition to positive retinotopic mapping in occipital regions supporting perception of the same stimulus. While our findings are consistent with this work, they add that positive retinotopic signals decrease along the unimodal-transmodal gradient, while negative retinotopic inputs are consistently present along this processing hierarchy (Margulies et al., 2016). This has implications for information processing within the DMN: rather than a simple transformation from a sensory to an abstract code, retinotopically-mapped inputs continue to be integrated at the highest

levels of the hierarchy, with a balance between activation and deactivation in response to visual inputs, which might reflect the way that DMN integrates information across all brain networks, including vision (Leech et al., 2025), while also supporting internally-generated experiences.

Retinotopic coding in higher-order networks was systematically associated with how neural activity tracked task focus, with distinct effects across default, control, and heteromodal systems. Positive retinotopic coding within DMN was associated with greater suppression of frontal control areas during focused comprehension, independent of sensory modality, and with increased occipital engagement during autobiographical recall. This pattern suggests that visual coupling within DMN supports focus by reducing reliance on executive control during comprehension while facilitating visual imagery during memory. These results add to the perceptual-memory dichotomy explored previously (Smallwood & Schooler, 2015; Steel et al., 2024) by showing that positive retinotopic coding is associated with perceptually-guided semantic tasks, as well as perceptually-decoupled aspects of memory, but through different cortical mechanisms.

In contrast, positive retinotopic coding within attentional control networks supported externally oriented focus during auditory comprehension but was associated with reduced engagement of medial temporal and anterior temporal regions during autobiographical memory recall, consistent with previous claims of functional opposition between perception and memory (Fox et al., 2005; Smallwood & Schooler, 2015; Spreng et al., 2009). Negative retinotopic coding in heteromodal networks also showed a strong effect of input modality (visual vs. auditory), and was associated with the efficient suppression of off-task regions when visual input was irrelevant, but increased recruitment of frontal control regions when visual information was task-relevant.

Our findings motivate a revision of how retinotopic information is understood within theories of perception, memory, and default mode function. Rather than simply providing a sensory trace, retinotopic coding persists into transmodal systems, where it could potentially influence the synthesis or gating of perceptual, semantic, and goal representations. Retinotopic coding within attentional control systems supports externally oriented focus while

constraining internally generated memory, consistent with competitive interactions between perceptual coupling and mnemonic processing (Andrews-Hanna, Smallwood, et al., 2014; Buckner & Carroll, 2007; Spreng et al., 2013). Within the DMN, visual coupling is linked to both externally-guided semantic comprehension and internally-generated memory: positive and negative retinotopic mapping might enable the flexible integration of conceptual representations with perceptual structure when relevant, and recruit imagery-based representations during recall. This view challenges accounts that position the DMN or its subsystems as purely perceptually decoupled; instead, its functional role depends on how perceptual information is integrated or suppressed across cognitive modes (Shao et al., 2024; Smallwood, Bernhardt, et al., 2021; Zhang et al., 2026).

The interpretations offered here are intended to describe systematic associations between retinotopic organisation and focus-related neural activity, rather than direct evidence that retinotopic organisation causally shapes functional engagement. These findings generate hypotheses regarding the potential contribution of intrinsic retinotopic organisation to sustaining focus during internally and externally oriented cognition, which could be further investigated using causal approaches, such as brain stimulation, neuropsychological studies, or longitudinal designs.

The current study collected participants' subjective focus rating but did not include objective task performance measures. Future studies could collect behavioural measures, such as comprehension or retrieval accuracy, and directly relate individual differences in retinotopic organization to fluctuations in reading or memory retrieval performance. In addition, classical retinotopic mapping paradigms typically rely on sparse visual stimulation to relate the brain responses to visual space and retinotopic maps in the brain (Lowndes et al., 2023; Mackey et al., 2017). The present analyses captured individual's stable intrinsic retinotopic connectivity patterns, rather than task-dependent fluctuations in retinotopic coding (Knapen, 2021). Future studies could further investigate how such fluctuations in retinotopic organization contribute to focussed comprehension or memory retrieval.

In summary, retinotopic coding is not confined to early visual or attentional systems, since we show that both positive and negative retinotopic effects persist within heteromodal

DMN and control networks. Task focus is associated not with the presence or absence of perceptual input, but with the distribution of retinotopically organised signals across large-scale networks. These positive and negative retinotopic patterns might allow the brain to sustain focus by balancing perception, memory, and control according to task demands.

Chapter 5. Discussion

5.1. Introduction

This thesis investigated the cognitive and neural mechanisms underlying the maintenance of task focus supported by semantic cognition. Semantic cognition supports not only the comprehension of external information, but also the generation of internally oriented thought (Jefferies, 2013; Keidel et al., 2018; Krieger-Redwood et al., 2016; Lambon Ralph et al., 2017; Smallwood et al., 2016). The default mode network (DMN) plays a critical role in both perceptual coupling and decoupling cognition through distinct functions of its subsystems (Fernandino & Binder, 2024; Gonzalez Alam et al., 2025; Shao et al., 2024; Smallwood, Turnbull, et al., 2021; Zhang et al., 2022). The empirical studies in this thesis examined mechanisms that sustain focus across different cognitive contexts, focusing on a non-semantic arithmetic task as well as memory-based comprehension and autobiographical memory retrieval tasks. This thesis also examined how thought content and perceptual coding influence task focus from behavioural and individual-differences perspectives.

Previous research on mind-wandering suggests that simpler tasks free up executive resources for internally generated thoughts, leading to increasing mind-wandering and activation of the DMN (Smallwood et al., 2008; Smallwood & Schooler, 2006). However, much of this work has focused on attention driven by external perceptual input and less is known about how focus is maintained in tasks that rely on memory representations, such as reading comprehension and memory retrieval. Accumulating evidence from reading studies indicates that mind-wandering actually increases with greater text difficulty (e.g., Feng et al., 2013; Kahmann et al., 2022; Soemer et al., 2019). Considering that involvement of semantic cognition in supporting reading, the neural mechanisms underlying task focus during reading may therefore involve the engagement of the DMN. In addition, the involvement of executive resources in such contexts may differ from that observed in most externally focused tasks. Based on these considerations, the specific aims of this thesis were:

- To investigate the neural mechanisms underlying the maintenance of task focus across different cognitive contexts. Chapter 2 addressed this question

using two fMRI studies. Study 1 examined whether the neural mechanisms supporting sustained focus differ between semantic (sentence comprehension) and non-semantic (arithmetic) tasks. Study 2 further investigated the mechanisms of sustained focus in two types of long-term memory-based tasks, namely comprehension and autobiographical memory retrieval, with a particular focus on the engagement of the DMN and executive control networks. Finally, a cross-study conjunction analysis was conducted to identify both shared and distinct neural mechanisms across different cognitive domains.

- To further examine the relationship between internally generated cognitive content during sustained semantic processing of different text types and difficulty, and how this relates to task focus and task performance. Chapter 3 used the multidimensional experience sampling (MDES) approach to characterize individual patterns of thought during text reading, and investigated how these thought patterns are associated with task focus and reading comprehension.
- To investigate whether intrinsic individual retinotopic coding patterns correlate with the neural mechanisms of sustained focus. Chapter 4 employed a retinotopic mapping task to characterize each participant's whole-brain visual coding. These measures were then related to focus-related neural activity observed during comprehension and autobiographical memory retrieval, in order to examine whether the retinotopic coding is associated with the engagement of DMN and executive control networks in sustaining task-related attention.

The discussion in this chapter is organized around the empirical findings of the present thesis. First, it provides a chapter-by-chapter summary of the main findings from the three empirical studies, outlining the key results of each experiment and their initial implications. Subsequently, these findings are integrated and linked to existing theoretical accounts along three core themes: (1) the mechanisms underlying the maintenance of task

focus, with a particular emphasis on the distinct roles of memory representational systems and executive control systems; (2) the role of the default mode network (DMN) in supporting cognitive coupling and decoupling; and (3) the relatively limited engagement of the multiple demand network (MDN) observed for memory engagement across the studies in this thesis. Finally, limitations of the present work are considered, together with directions for future research.

5.2. Summary of each chapter

5.2.1. Chapter 2

In this chapter, we conducted two neuroimaging studies to examine the neural mechanisms that sustain focus during different cognitive processes. In Study 1, participants performed comprehension (semantic) and arithmetic (non-semantic) tasks that varied in difficulty, to investigate the neural mechanisms supporting focus in externally oriented cognition across semantic and non-semantic tasks. During the fMRI scan, participants were first asked to generate personal thoughts linked to a cue phrase. They then either read factual sentences or solved arithmetic problems (serial addition). Task focus ratings were recorded after each trial. Participant focus was higher for easy than difficult comprehension tasks, but the reverse was true for arithmetic, with higher focus for difficult than easy addition. Parametric analyses of task focus showed that higher focus during comprehension was associated with stronger engagement of lateral temporal regions within the dorsal medial DMN subsystem, along with greater disengagement of bilateral cingulate and frontal regions within control and salience networks. In the arithmetic task, higher focus was associated with increased activation in motor and visual cortex, along with increased deactivation in medial visual and right motor regions. These findings suggest distinct neural mechanisms underlying sustained focus in comprehension and arithmetic: comprehension engaged semantic memory systems while suppressing executive control regions, whereas high focus during arithmetic was associated with activity in sensory-motor regions.

Study 2 was performed to further examine the mechanism supporting sustained focus during externally directed reading and internally generated thoughts. The procedure was similar to Study 1, participants first retrieved their autobiographical memory linked to a cue

word, then either kept thinking about these personal memories or read factual sentences. Sentences for comprehension were presented in the visual or auditory modality; memory retrieval was performed while ignoring visual or auditory sentences, or without distraction. Task focus ratings were recorded at the end of each trial. Overall, participants were more focussed during the comprehension of visual and auditory sentences than during the internal memory retrieval task that required ignoring sentences. Within the internal memory retrieval task, focus was highest when retrieval occurred without distraction, whereas memory retrieval in the presence of auditory sentence interference was associated with the lowest levels of task focus (i.e., participants found the auditory sentences the hardest to ignore). Neuroimaging results showed that higher focus during both auditory and visual comprehension was associated with greater recruitment of the dorsal medial DMN subsystem (lateral temporal regions), alongside stronger deactivation in the control and salience networks (medial anterior cingulate cortex and paracingulate cortex). This pattern is consistent with the findings from Study 1 for the comprehension task. For the internal memory retrieval task, greater focus was associated with increased engagement of the medial temporal DMN subsystem (medial temporal regions). Similar to the comprehension task, more focused memory retrieval was also accompanied by stronger deactivation in the control and salience networks.

The conjunction analysis across Studies 1 and 2 confirmed that during comprehension higher focus was associated with increased activation in the dorsal medial DMN subsystem, along with stronger deactivation of the core DMN and executive control networks. In addition, distinct mechanisms were observed for arithmetic versus memory-based tasks. Greater activation in lateral temporal regions was associated with higher focus during comprehension but lower focus during arithmetic, whereas greater activation in medial temporal regions was associated with higher focus during autobiographical memory retrieval but lower focus during arithmetic. Functional connectivity analyses further demonstrated that higher focus during comprehension was associated with increased segregation between regions of higher activation (e.g., lateral temporal cortex) and regions of greater deactivation (e.g., executive control networks).

These findings suggest that memory-based and non-memory-based tasks rely on distinct neural mechanisms to sustain attention. For memory-based tasks, including comprehension and autobiographical memory retrieval, sustained attention depends on the engagement of task-relevant representational systems: in our study, semantic tasks relied on semantic representation networks within the dorsal medial DMN subsystem, whereas internally oriented cognition (e.g., autobiographical retrieval) tended to engage the medial temporal DMN subsystem. Importantly, memory-based tasks share a common mechanism involving the disengagement of executive control networks during sustained attention. In contrast, non-semantic tasks, such as arithmetic, rely more strongly on sensorimotor regions. Finally, functional connectivity results suggest that sustained attention during reading arises from decoupling between semantic representation systems (dorsal medial DMN subsystem) and executive control networks.

5.2.2. Chapter 3

The fMRI studies in Chapter 2 suggested that maintaining memory-based task focus relies more on the sustained engagement of memory representational systems, than on executive control mechanisms. This challenges accounts that equate attention with control-driven processes, and instead points to a central role for systems involved in semantic representation and integration. If representational systems underpin task focus, then engagement is likely shaped by the content and structure of ongoing thought, particularly the extent to which thoughts are semantically coherent and aligned with the task. The next study examined the nature of thought patterns at the behavioural level, especially in relation to mind-wandering. In this study, participants completed two comprehension experiments with factual texts and short stories that varied in difficulty. Self-caught mind-wandering was recorded during reading, and multidimensional experience sampling (MDES) was used to capture the patterns of ongoing thoughts after reading. At the end of each trial, three questions regarding the current text were used to assess participants' comprehension accuracy. Across both experiments, more difficult texts were associated with increased mind-wandering, and comparisons between experiments showed that expository (factual) texts elicited more mind-wandering than narrative texts. Difficult expository texts were further associated with a higher

frequency of task-unrelated thoughts, particularly those related to future problem-solving and intrusive sounds, whereas easy narrative texts elicited more deliberate, detailed thoughts. Overall, expository texts elicited the most mind-wandering – with future problem-solving and past knowledge-related thoughts, while mind-wandering in narrative texts was much lower and so thoughts were more deliberate and detailed (i.e., focused on the text). Importantly, both future problem-solving and intrusive sound-related thoughts were associated with poorer text comprehension, whereas deliberate, detailed thoughts were linked to better comprehension. These effects on comprehension were also more pronounced in expository texts.

These results first reveal a difficulty effect in reading tasks that is consistent with the behavioural findings from fMRI studies in Chapter 2: more difficult texts lead to increased mind-wandering. This effect is consistent across text types, regardless of whether the texts are expository or narrative. This aligns with many previous studies on mind-wandering during reading (Feng et al., 2013; Kahmann et al., 2022; Soemer et al., 2019). Importantly, we found that the nature of thoughts varies across different levels of difficulty and text types. Task-unrelated thoughts occurred more frequently in difficult expository texts and were associated with poorer reading comprehension, whereas task-related thoughts were more common in easy narrative texts and were linked to higher levels of comprehension. Taken together, these findings suggest that, during reading, the alignment between the content of thoughts and the semantic goals of the text is critical for maintaining attention and influences reading outcomes, highlighting the importance of the alignment between ongoing thoughts and the current task for successful comprehension.

5.2.3. Chapter 4

The final empirical study examined how perceptual information modulates task driven attention during external semantic processing and internal autobiographical memory retrieval. The same group of participants used in Study 2 of Chapter 2 completed a retinotopic mapping task. The results showed that, beyond classic visual areas, retinotopic coding of both positive- and negative-amplitude population receptive fields (pRFs) extended into higher-order cortical regions, including the temporal, parietal and frontal cortices. With the exception of motor areas, the tuning strength of positive pRFs (+pRFs) decreased along the principal

gradient from unimodal to transmodal cortex (Margulies et al., 2016), as confirmed by spatial permutation test. In contrast, negative pRFs ($-pRFs$) did not show a statistically significant relationship with the principal gradient. As expected, $+pRFs$ also showed stronger tuning strength than $-pRFs$ in visual and dorsal attention networks (DAN) based on the Schaefer 400 parcels for 7 networks. Pairwise t-tests across 7 networks, ordered along the principal gradient, revealed that tuning strength was highest in the visual network, followed by DAN; lower but comparable levels were observed in the ventral attention network (VAN), control network and DMN, whereas the limbic network showed the weakest tuning. The somatomotor network was an exception to this overall pattern. To further understand these results, a principal component analysis (PCA) of positive- and negative-amplitude R^2 values across the Schaefer 17-network parcellation identified three main components (i.e., default/limbic $+pRFs$, control attention $+pRFs$, and heteromodal $-pRFs$). We then tested whether these components were associated with focus-related neural activity during comprehension and autobiographical memory retrieval. The result showed that:

- a. Stronger positive retinotopic coding within the default mode and frontal limbic network was associated with greater suppression of frontal control regions during focused comprehension (focus-negative regions that deactivate with focus), and with increased occipital engagement during autobiographical memory recall (focus-negative regions that deactivate with focus).
- b. Stronger positive retinotopic coupling in control and attention networks was associated with enhanced focus-related activation in sensorimotor, visual and frontal regions during auditory comprehension, but with attenuated focus-related activation in memory regions during autobiographical memory recall without distraction.
- c. Stronger negative retinotopic coding in heteromodal systems was associated with greater suppression of task-irrelevant regions during auditory comprehension, but with increased engagement of frontal control regions and

reduced focused-related activation in anterior temporal lobe (ATL) during visual comprehension.

These findings revealed that the engagement of the DMN and control networks during sustained attention in comprehension and autobiographical memory retrieval is constrained by an individual's embedded retinotopic coding. Individuals with stronger positive retinotopic coding within the DMN/limbic system tend to rely more on visual representations to support task performance. During memory recall, enhanced visual coupling attenuated the typical suppression of visual regions with increasing focus. In contrast, during comprehension tasks, visual information may penetrate semantically related DMN regions to support task processing, more effectively suppressing task-irrelevant executive control regions. In the control network, stronger positive retinotopic coding in control and attention networks may bias cognitive processing toward externally driven inputs, thereby interfering with internally generated memory retrieval processes. Finally, stronger negative retinotopic coding within heteromodal systems appears to support more efficient suppression of task-irrelevant regions when visual information is not relevant to the task. When visual information becomes task-relevant, negative encoding instead modulates the balance between suppression of control regions and engagement of semantic regions.

5.3. Discussion

5.3.1. Sustaining Focus during comprehension and memory retrieval

Traditional accounts have largely conceptualised sustained attention as the outcome of top-down executive control, typically associated with the engagement of frontoparietal control systems and the suppression of default-mode processing (Fox et al., 2005; McVay & Kane, 2012; Smallwood, 2013; Smallwood & Schooler, 2006). Lapses of attention are often characterised as failures of control, accompanied by increased internally oriented activity that is decoupled from the external task (Kane & McVay, 2012; McVay & Kane, 2010). In this thesis, we reconsider the mechanisms supporting task focus and extend current accounts through three empirical chapters.

Chapter 2 first revealed distinct difficulty effects for arithmetic and comprehension tasks. In arithmetic, participants reported lower levels of focus during easy tasks than during

hard ones, which is consistent with accounts suggesting that simple tasks either leave spare executive resources available for mind-wandering (Smallwood & Schooler, 2006) or increase the likelihood of mind-wandering due to failures of executive control (McVay & Kane, 2010). The pattern was reversed for comprehension: participants reported greater task focus during easy comprehension tasks than during hard ones. The overlap between difficulty effects and focus effects at the neural level also reveals distinct task focus mechanisms. In arithmetic tasks, higher levels of task focus were associated with increased activation in visual and motor regions, which were also more strongly engaged during more difficult trials. This pattern is consistent with prior evidence showing that arithmetic engages visual-symbolic processing and motor-related systems (Domahs et al., 2010; Noël, 2005; Vinci-Booher et al., 2021). Poorer attention during arithmetic was associated with increased activity in medial temporal regions of the DMN subsystem, which has been linked to the generation of internally oriented thought and mind wandering (Andrews-Hanna, Smallwood, et al., 2014; Shao et al., 2024; Zhang et al., 2022). Notably, these regions also showed greater activation during easier compared to more difficult arithmetic tasks. In comparison, semantic tasks revealed a distinct neural mechanism for maintaining task focus. During comprehension, greater task focus was associated with increased recruitment of semantic processing regions in the lateral temporal cortex, overlapping with regions that showed greater activation during easy relative to hard comprehension tasks. These findings indicate that semantic (comprehension) and non-semantic (arithmetic) tasks appear to recruit distinct cognitive and neural mechanisms to support sustained attention.

The second study in Chapter 2 further revealed neural mechanisms of sustaining focus in memory-based tasks that differ from those observed in arithmetic. The focus effects in comprehension were replicated across datasets: greater focus was associated with increased engagement of lateral temporal cortex, consistent across visual and auditory modalities. Similarly, in autobiographical memory retrieval tasks, sustained attention was associated with increased activation in medial temporal regions implicated in episodic memory retrieval. These results indicate that sustained attention in meaning-based tasks is associated with the continued engagement of semantic and memory-related systems, rather than increased

recruitment of control or salience networks. Notably, activity within control and salience systems was relatively attenuated during periods of stable task engagement. This suggests that maintaining attention on memory representations may not simply reflect a reduced reliance on systems typically associated with external monitoring (Duncan, 2010; Menon & Uddin, 2010; Smallwood & Schooler, 2015), but may instead reflect a role of task-relevant representations in supporting the maintenance of attention. In particular, during comprehension, higher levels of task focus were associated with greater functional segregation between networks, characterised by increased involvement of the DMN alongside reduced engagement of executive control systems. This pattern may reflect the contribution of coherent semantic representations to maintaining task-relevant context over time. This continuity of representations may reduce the need for continuous top-down regulation while still supporting integration of externally presented information (D'Esposito & Postle, 2015; Stokes, 2015). These findings challenge the assumption that executive control is the primary mechanism for maintaining focus, and instead highlights the role of representational continuity in supporting task focus.

If memory-based representations play a central role in sustaining focus, then the content of these representations may also be critical. Chapter 3 directly addressed this question by examining heterogeneous patterns of thought during reading. Rather than treating mind-wandering as a unitary construct, the present findings revealed substantial variability in ongoing thought (Bellana et al., 2022; Mulholland et al., 2023; Smallwood, Turnbull, et al., 2021; Wallace et al., 2025). Our results first replicated the difficulty effect reported in Chapter 2 in the context of text reading, namely the finding that more difficult texts elicited more mind-wandering. This finding is inconsistent with theories positing that executive control maintains task focus and prevents mind wandering: by this account, greater executive resources available during easy texts would allow more resources to be diverted toward internally generated thoughts (Smallwood et al., 2008; Smallwood & Schooler, 2006). In contrast, our results suggest that hard texts showed increased mind-wandering in both factual and story text comprehension. In addition, narrative texts elicited less mind-wandering compared to factual texts, which may be related to the more coherent narrative structure of

story-based texts and their resemblance to real-world social experiences (Clinton et al., 2020; Mar et al., 2021). Furthermore, analyses of thought content revealed the importance of the nature of thought content for task focus. Compared with easy factual texts, difficult factual texts were associated with significantly higher scores for off-task thoughts; similarly, easy narrative texts scored higher for on-task thoughts. Furthermore, deliberate and detailed task-related thinking, were associated with higher levels of task focus and enhanced comprehension. In contrast, thoughts that were decoupled from the task context, such as future-oriented or task-unrelated thinking, were associated with reduced task focus and poorer performance. This indicates that attention is closely linked to the extent to which ongoing mental content is aligned with external task information. In this sense, what individuals think about plays an important role in whether attention is maintained or disrupted.

Findings in Chapter 4 further indicate that visual organization embedded within higher-order systems is associated with modulation of the neural processes supporting sustained attention. Individual differences in retinotopic coding were related to variability in the neural activity underlying task focus during both comprehension and autobiographical memory recall. Although traditional accounts often assume a hierarchical progression from concrete sensory processing to abstract representations (Margulies et al., 2016; Popham et al., 2021), accumulating evidence suggests that higher-order regions, including the DMN and hippocampus, retain sensitivity to low-level retinotopic information (Knapen, 2021; Silson et al., 2016; Silson et al., 2021; Szinte & Knapen, 2020). Recent evidence suggests that retinotopic coding may provide a scaffold that links perceptual and mnemonic systems, structuring their interactions and supporting dynamic communication between them (Groen et al., 2022; Steel et al., 2024). Consistent with this account, Chapter 4 demonstrated that the relationship between neural activity and task focus was associated with individual differences in the strength of positive and negative retinotopic coding across large-scale networks. Specifically, individuals exhibiting stronger positive retinotopic coding within the DMN showed greater suppression of control networks during sustained attention to comprehension tasks. In contrast, individuals with stronger positive coding in executive control networks exhibited reduced involvement of medial temporal regions during recall without distraction.

Moreover, individuals characterized by stronger negative coding patterns across heteromodal regions showed decreased engagement of lateral temporal regions and increased recruitment of executive control during sustained visual comprehension. Together, these findings indicate that individual differences in visual organization across large-scale networks modulate how focus is supported by distributed neural activity, shaping the engagement of memory representational and executive control during comprehension and memory retrieval.

Our findings complement existing theories of task focus rather than conflicting with them. Within classical accounts that emphasize the role of executive control in anchoring attention to external goals, attention is supported by coordinated large-scale networks: the dorsal and ventral attention systems direct attention in a goal-driven or stimulus-driven manner, the frontoparietal control network enhances perceptual processing of task-relevant external information and the salience network detects behaviourally relevant events (Corbetta & Shulman, 2002; Dosenbach et al., 2007; Petersen & Posner, 2012). These models have been highly successful in explaining how attention is maintained toward external targets, particularly in paradigms involving highly structured external input, such as target detection and simple discrimination tasks. In contrast, the present thesis addresses a different question: how is attention maintained when task demands are not fully specified by external input, and instead coherence must be constructed from long term memory? Such situations require sustained, internally generated semantic or episodic representations to support ongoing comprehension. Recent work on mind wandering and the DMN provides an important extension to traditional accounts (Christoff et al., 2016; Seli et al., 2016; Smallwood, Bernhardt, et al., 2021). Evidence suggests that fluctuations in attention reflect not only failures of external selection, but also dynamic changes in internally generated thought (Esterman et al., 2013; Esterman et al., 2014; Kucyi et al., 2017). Moreover, the functional impact of mind wandering depends critically on the content of thought, with some internally generated thoughts supporting ongoing task performance (P. Seli et al., 2018; Turnbull, Wang, Schooler, et al., 2019; Wang et al., 2018). Consistent with this, our results highlight the importance of task-related memory representations in sustaining focus, reflected neurally in the sustained engagement of focus-related memory representations, and behaviourally in task-

relevant thought content that facilitates task performance. This suggests that theories emphasizing executive control may overestimate its role in naturalistic cognition, particularly in tasks such as reading that rely heavily on internally constructed representations. Therefore, it is important to move beyond accounts of sustained attention that focus solely on top-down control, and to consider how focus states are shaped by the alignment of underlying representational systems and external content, and modulated by individual differences in visuospatial coding.

5.3.2. The Role of the DMN in Perceptually Coupled and Decoupled Cognition

A large body of research has demonstrated that the default mode network (DMN) supports internally oriented cognitive states, in which cognition is decoupled from perceptual input in the external environment, such as during memory retrieval and mind-wandering (Andrews-Hanna, 2012; Murphy et al., 2018; Spreng et al., 2009; Zhang et al., 2022). However, accumulating evidence also shows that the DMN is engaged during externally oriented, perceptually driven tasks, including reading comprehension (Binder et al., 2009), semantic decisions (Humphreys et al., 2015; Krieger-Redwood et al., 2016; Shao et al., 2024) and demanding working memory tasks (Spreng et al., 2014; Vatansever et al., 2015). An influential account attempts to reconcile these findings by proposing that different DMN subsystems support distinct modes of cognition (Andrews-Hanna, Smallwood, et al., 2014; Shao et al., 2024; Souter et al., 2024; Zhang et al., 2022). For example, the dorsal medial (DM) subsystem has been linked to perceptually coupled processing, whereas the medial temporal (MT) subsystem is thought to support perceptually decoupled cognition. This framework suggests that the DMN can flexibly shift between perceptually coupled and decoupled states depending on task demands, through its intrinsic links with sensory, executive control systems, or the hippocampus (Dixon et al., 2018; Ferris et al., 2025; Krieger-Redwood et al., 2016; Zhang et al., 2022).

Our findings partially support this perspective by showing that the engagement of DMN can maintain both perceptually coupled and decoupled cognitive states (Chapter 2). High focus during comprehension and autobiographical memory retrieval showed different DMN subsystem engagement, consistent with the subsystem account: perceptually coupled

reading engages the DM subsystem, whereas perceptually decoupled memory retrieval engages the MT subsystem. We also demonstrated that during comprehension, the lateral temporal region within the DM subsystem can sustain focus by decoupling from the executive control network. This finding supports the view that the DMN contributes to perceptually coupled cognition by sustaining semantic representation, rather than through continuous top-down control.

In addition, the retinotopic findings highlight a more complex pattern by revealing the critical role of individual differences. According to the traditional view, regions engaged in perceptually coupled tasks should show stronger visual coupling, whereas regions engaged in perceptually decoupled tasks should show weaker visual coupling. The results in this thesis do not support this binary dissociation. Specifically, we identified a pattern of positive pRFs within the DMN (Chapter 4), indicating a stable neural property reflecting the degree to which these higher-order regions retain structured visual information. Furthermore, individual differences modulated how the DMN supported task focus in perceptually coupled (comprehension) versus decoupled (autobiographical memory retrieval) tasks: individuals with higher expression of positive pRFs within the DMN showed greater suppression of frontal control regions during focused comprehension, independent of sensory modality. This suggests that visual coupling in the DMN during reading does not simply reflect sensory input processing; rather, it may facilitate sustained focus by reducing reliance on executive control systems. In contrast, during autobiographical memory retrieval, individuals with higher expression of positive pRFs in DMN showed increased engagement of occipital regions, suggesting a role in supporting visual imagery. Thus, the presence of retinotopic coding within the DMN does not map cleanly onto a coupled-versus-decoupled distinction. The same retinotopic organization within DMN serves different functions depending on task context: during comprehension, it may help facilitate sustained focus by reducing reliance on executive control systems; during retrieval, it may help couple memory representations with visual imagery. In this way, positive pRFs support both perceptually guided semantic processing and perceptually decoupled aspects of memory, albeit through distinct cortical mechanisms. Rather than reflecting a binary functional segregation between DMN

subsystems, our results indicate that DMN involvement in perceptual coupling and decoupling reflects a dynamic and flexible allocation of processing resources in which retinotopic coding modulates the engagement of the DMN and its interactions with other large-scale networks depending on task demands. These findings are consistent with growing evidence that higher-order cortical regions retain structured visual information, which may provide a scaffold for communication between long-term memory systems and visual systems across both perceptually coupled and decoupled states (Groen et al., 2022; Knapen, 2021; Steel et al., 2021; Steel et al., 2024).

Taken together, our results suggest that the engagement of the DMN in perceptual coupling and decoupling is not fully captured by a simple functional segregation. During cognitive processes involving perceptual coupling and decoupling, the role of DMN is to maintain task-relevant representation, with flexible coupling or decoupling of perceptual or executive control networks. Importantly, this engagement is not uniform across individuals. Our findings demonstrate that individual difference in the whole-brain retinotopic structure, particularly the extent to which positive pRFs are expressed within the DMN, are associated with how the DMN supports task focus in perceptually coupled and decoupled contexts.

5.3.3. The Engagement of the Multiple-Demand Network in Sustained Cognition

A notable finding in this thesis is the relatively limited engagement of the multiple-demand network (MDN) during sustained task performance. This observation appears to contrast with dominant accounts of cognitive control, which suggest that MDN activity scales with task demands and is consistently recruited during effortful cognition (Fedorenko et al., 2013; Turnbull, Wang, Murphy, et al., 2019; Turnbull, Wang, Schooler, et al., 2019). Within this framework, more demanding tasks—such as harder mathematical problems or semantically complex sentences—are expected to elicit stronger and more sustained activation in domain-general control regions. However, the present results do not support a straightforward relationship between task difficulty and MDN engagement (Chapter 2). In Study 1, increased difficulty in the arithmetic task did not correspond to stronger MDN engagement, nor was it directly associated with task focus. Similarly, in the semantic task, more difficult sentences did not lead to greater involvement of control-related regions, nor did

they reliably enhance on-task states. These findings suggest that MDN engagement neither scales with increasing task demands nor consistently supports the maintenance of task focus, pointing instead to alternative mechanisms underlying attentional maintenance.

One possible explanation lies in the nature of the task itself. Sustained attention tasks, while extended in duration, may rely more on stable, ongoing processing rather than dynamic reconfiguration or high levels of cognitive effort (Christoff et al., 2016; Smallwood & Schooler, 2015). Study 2 in Chapter 2 showed that during sustained cognition based on long-term memory, such as reading or autobiographical recall, memory-related systems were engaged, while executive control regions were consistently suppressed during periods of sustained attention. In particular, maintaining attention during comprehension was associated with stronger decoupling between lateral temporal regions involved in semantic processing and executive control networks. This pattern suggests that sustained task focus in our paradigm depends less on continuous top-down control and more on the maintenance of coherent semantic representations (Chang et al., 2022; Lanzoni et al., 2020; Simony et al., 2016). Supporting this interpretation, findings from Chapter 3 demonstrate that task conditions with simpler and more coherent semantic input were associated with higher levels of task focus and better comprehension. These states were further characterized by deliberate, detailed, on-task thought patterns. Therefore, in such contexts, once task-relevant representations are established, performance may proceed with relatively low demand for active control, reducing the need for continuous MDN recruitment. This is consistent with accounts proposing that cognitive control operates by modulating and maintaining task-relevant representations, and is engaged flexibly depending on contextual demands rather than being continuously sustained (Cole et al., 2013; Panichello & Buschman, 2021; Rosero Pahi et al., 2020; Woolgar et al., 2011). These accounts are also compatible with the predictive coding framework, in which the stabilization of task-relevant representations can be understood as establishing reliable priors, thereby minimizing prediction error and reducing the necessity for continuous top-down control (Clark, 2013; Feldman & Friston, 2010).

Another thing that needs to be considered is the distinction between different kinds of control. In contrast to the domain-general executive control supported by bilateral MDN (Duncan, 2010; Fedorenko et al., 2013), a distinctive left-lateralised semantic control network is specifically recruited when semantic representations must be selected, maintained or manipulated (Jackson, 2021; Jefferies, 2013; Jefferies & Wang, 2021). In Chapter 2 (Study 1), we found that higher levels of task focus during comprehension were associated with greater engagement of the left IFG, a key node of the semantic control network, suggesting a role of this region in supporting sustaining attention to external inputs requiring access to semantic memory. Critically, however, this IFG engagement did not vary with text difficulty. Comparing easy and difficult comprehension tasks revealed no significant difference in semantic control activation, nor did a parametric modulation analysis show any difficulty-related effect (see Chapter 2, Supplementary Materials). The engagement of left IFG in comprehension was not driven by increased task demands, nor accompanied by broader semantic control recruitment. This suggests that the observed IFG activity may be better characterized as supporting the maintenance of coherent semantic representations during ongoing comprehension, consistent with continuous engagement of language-related networks (Fedorenko et al., 2011), rather than demand-driven control processes typically associated with the broader semantic control network (Lambon Ralph et al., 2017).

Overall, the present results do not support the view that MDN implements top-down control to sustain task focus in memory-based processes. The results in this thesis suggest that such tasks may rely less on sustained executive control once stable representations are established, consistent with mechanisms based on sustained semantic maintenance rather than continuous executive engagement.

5.4. Limitations and directions for future research

The present thesis has several limitations that should be acknowledged. First, the fMRI findings reported in this thesis identify associations between focus states and patterns of activity within the DMN, executive control networks, and perceptual systems. However, these findings did not establish causal relationships between neural activity and the maintenance of task focus (Bielczyk et al., 2019; Henson, 2005). For example, while sustained focus during

comprehension and autobiographical memory retrieval was associated with increased engagement of representational regions and reduced activity in control networks, it remains unclear whether these neural patterns are necessary for maintaining focus. From a causal perspective, future research could complement these findings by employing methods that allow for stronger inference regarding necessity and sufficiency, such as transcranial magnetic stimulation (TMS), or lesion-based approaches to clarify the causal contributions of these systems to sustained focus. Second, the assessment of thought content in the present thesis was based on MDES, which captures participants' subjective experience after each text in our experiments. While MDES provides valuable insight into the content of ongoing cognition, it relies on self-report and therefore may reflect related to multiple processes (Grund et al., 2024; Unsworth et al., 2024). In addition, the temporal resolution of experience sampling is limited, making it difficult to capture rapid fluctuations in attentional states and thought dynamics. Future studies could address this limitation by adopting higher-frequency sampling approaches or combining MDES with neurophysiological techniques that provide higher temporal resolution. In particular, integrating experience sampling with magnetoencephalography (MEG) or eye tracking may allow for a more fine-grained characterization of the temporal dynamics of thought and attention (Foulsham et al., 2013; Martinon et al., 2019). Third, the present thesis focused primarily on comprehension and autobiographical memory retrieval as representative tasks involving internally generated representations. While these tasks are theoretically motivated and widely studied, they represent only a subset of possible cognitive contexts. Future research could extend the current accounts to a broader range of task domains, including more naturalistic and ecologically valid settings, in order to test the generalizability of the representational account of sustained focus.

Many thesis findings also remain open to alternative interpretations. In Chapter 2, there were no clear differences between sensory modalities; sustaining focus during both visual and auditory comprehension was associated with shared semantic processes. One possible explanation is that once stable internal representations are established, the influence of external sensory input on attention may be reduced (D'Esposito & Postle, 2015; Stokes,

2015), given the multimodal nature of conceptual knowledge (Lambon Ralph et al., 2017). This interpretation appears to contrast with evidence from retinotopic mapping, which highlights the importance of concrete visual information in sustaining attention. Future research should therefore further investigate whether modality-specific processing pathways contribute to sustained attention, and whether such effects are masked by higher-order semantic integration processes. In addition, the present study did not directly link the contents of ongoing thought during different tasks with their neural correlates. In Chapter 2, the overlap in the effects of low focus in arithmetic and high focus in autobiographical memory might suggest common types of thought in these contexts, but this was not directly assessed. The similarities and differences between on-task thought in reading and memory tasks and off-task thought in arithmetic remain unclear: internally generated thoughts are often associated with medial temporal regions, yet semantic processing is also likely to play a critical role in shaping their neural representation (Irish & Piguet, 2013; Vatansever et al., 2021). Future work should more directly examine how task-related and task-unrelated thoughts are represented in the brain, and how these representations map onto large-scale networks such as the DMN and executive systems. Finally, although sustaining focus was closely related to task performance, the two constructs are not equivalent (Smallwood & Schooler, 2015). The present study examined focus ratings, but did not include an objective measure of behavioural performance. Future research should therefore investigate whether different neural mechanisms underlie successful versus failed comprehension or calculation, particularly in more demanding task conditions.

The findings in this thesis have several potential practical implications for education and the understanding of individual differences in attention. First, the results suggest that sustaining focus during reading is associated with the engagement of task-relevant representations, which may vary depending on text type and difficulty. Previous research has shown that narrative texts often support more coherent mental representations and are associated with more stable engagement compared to expository texts (Best et al., 2008; Clinton et al., 2020). In line with this, the present findings suggest that narrative reading exhibited less mind-wandering and was more related to deliberate and detailed thought that

aligned with the content of the text. This highlights the importance of considering text characteristics in educational settings, particularly textual clarity and coherence, when designing materials that aim to support sustained attention and comprehension. Second, the findings on thought content suggest that mind-wandering is not a unitary phenomenon. Task-unrelated thoughts, such as future-oriented problem solving, were associated with poorer comprehension, whereas task-related, detailed thought was linked to improved performance. This distinction is consistent with previous work showing that the impact of internal generated thoughts on performance depends on its content and context (Mulholland et al., 2023; Vatansever et al., 2020; Wang et al., 2017). These findings suggest that educational strategies may benefit not only from reducing mind-wandering in general, but also from promoting forms of internally generated thought that are aligned with task goals, such as encouraging elaboration or mental simulation during reading. Third, the identification of individual differences in perceptual encoding and thought patterns suggests that variability in sustaining focus may be partly related to broader cognitive characteristics. This may have relevance for understanding attentional differences across individuals, including those observed in conditions such as ADHD, which are often associated with increased variability in attention and mind-wandering (Fortenbaugh et al., 2017; Seli et al., 2016; Yamashita et al., 2021). Although the present findings do not directly address clinical populations, they are consistent with the view that differences in internally generated cognition and perceptual organization are associated with differences in maintaining focus. Finally, these findings may inform approaches to supporting focus during reading. For example, strategies that encourage task-relevant processing, such as guiding readers to generate detailed, text-related representations, may be associated with improved comprehension, whereas reducing the occurrence or impact of task-unrelated thoughts may support more stable attention. Taken together, these observations suggest that sustained attention in real-world contexts may be better understood by considering not only whether attention is maintained, but also the nature of the representations and thoughts that are engaged during task performance.

5.5. Conclusion

The present thesis systematically investigated the mechanisms underlying the maintenance of task focus during semantic cognition, and proposed an account that task focus is sustained through the continuous maintenance of task-relevant representations, which distinguishes itself from traditional executive control models. First, the findings revealed that for memory-based tasks such as reading comprehension and autobiographical memory retrieval, the core mechanism of sustained focus is the continuous engagement of task-relevant memory representation systems. This is supported by the dorsal medial DMN for semantic representations and the medial temporal DMN for episodic memory, accompanied by decoupling from executive control networks. In contrast, non-semantic arithmetic tasks relied on fundamentally different mechanisms, highlighting the task-dependent nature of attentional maintenance mechanisms. Second, through detailed analysis of thought content, the behavioural study uncovered the heterogeneity of ongoing thoughts during reading: task-unrelated thoughts (e.g., future problem solving) impaired comprehension, whereas task-relevant deliberate detailed thoughts facilitated comprehension, indicating that the quality of attention depends critically on the content of thought rather than simply on whether attention has wandered away from the task. Third, by examining individual differences in retinotopic coding, the present thesis found that individuals' intrinsic retinotopic coding patterns significantly constrained the engagement of higher-order cognitive networks, including the DMN and control networks, during focussed comprehension and autobiographical memory retrieval. Together, the present thesis argues that sustaining task focus, particularly in tasks supported by semantic cognition, can be understood as a process of stabilizing and maintaining task-relevant representations. Rather than being captured by binary distinctions between the DMN and control networks, or between perceptual systems and DMN subsystems, this process is implemented through dynamic interactions between the DMN and executive control networks, and is further shaped by individuals' perceptual organization and the content of ongoing thought.

Appendices

Supplementary Information for Chapter 2

Supplemental Methods

Procedure.

Study 1: Participants first generated their personal memories linked to autobiographical cue phrases outside the scanner. They were asked to think about a personal memory involving someone they knew, a show, song, or event, future plans or personal ideas. They then completed twelve practice trials to familiarize themselves with the paradigm. In the scanner, as shown in Figure 2.1A, each trial started with a fixation cross (1-3 s) at the centre of the screen, followed by an autobiographical cue phrase lasting 3 s. During the presentation of the cue phrase, participants brought to mind their detailed personal memories related to this item. Next, a jittered fixation (1-3 s) was presented before the sentences or numbers.

Following the fixation, the main trial began with presentation of stimuli lasting for 9 s. Stimuli consisted of either sentences or numbers. Sentences were presented on 15 successive slides, with each one lasting 600 ms, combining short words on a single slide (e.g., “such as”) or presenting articles and conjunctions together with nouns (e.g., “a minute”). Numbers were presented on every other slide, with a blank screen in between, resulting in a total of eight number slides. Each trial was followed by a jittered fixation (1-3) and a task focus rating question. Participants were required to rate their task focus on a 7-point scale of from 1 (i.e., think about other things) to 7 (i.e., think about the meaning of the sentence or the ongoing addition of the numbers) within 2 s. Responses were made using two button boxes, with the left hand indicating lower ratings and the right hand indicating higher ratings.

Each condition contained 25 trials and the stimuli were presented across four runs, with each containing 25 trials. Each trial lasted on an average of 20 s. The whole experiment lasted 32 minutes. Trials were presented using a mini-block design: within each run, all trials of the same condition were presented consecutively in a pseudorandom order, and the order of conditions was counterbalanced across runs.

Study 2: This study occurred across two consecutive days. On day 1, participants generated their personal memories linked to autobiographical cue words (e.g., sea) outside the scanner. They were asked to identify specific events that they were personally involved in and to provide as much detail about these events as they could, including when and where the event took place, who was involved, what happened, and the duration. They were asked to type these details into a spreadsheet, which ensured that comparable information was recorded for different cue words.

On day 2, before entering the scanner, participants were asked to review their generated memories to ensure they were easily accessible when presented with the cue word in the scanner. Next, they performed ten practice trials to familiarize themselves with the paradigm. In the scanner, participants engaged in internal recall of their memories when presented with a cue word (i.e., participants did not speak in the scanner), and also read and listened to factual sentences in a comprehension task. As shown in Figure 2.1C, each trial started with a fixation cross (1-3 s) in the centre of the screen, followed by a written and spoken autobiographical memory cue word lasting 2 s. During the presentation of the cue word, participants brought to mind their detailed personal memories relating to this item. Next, the task instruction (i.e., COMPREHEND or RECALL) was presented for 1 s, in either a visual (i.e., text) or auditory (i.e., voice) format. Following the task instruction, the main trial began, with presentation of stimuli lasting for 7.8-10.2 s, with an average of 9 s. Stimuli consisted of either (1a) visual or (1b) auditory sentences or (2a) a series of x's (visual) or (2b) white noise (auditory). The visual sentences were presented on 13-17 successive slides, with each one lasting 600 ms, combining short words on a single slide (e.g., "such as") or presenting articles and conjunctions together with nouns (e.g., "the heat"). The auditory sentences were presented naturalistically, with the sentence unfolding as the speaker intended. The visual instructions and sentences were presented together with white noise, and the auditory instructions and sentences were presented together with letter strings (e.g., XXXXX), which varied in length (i.e., XXX ; XXXXXX, etc), so that sensory inputs were presented in both visual and auditory channels across all conditions. On memory recall trials without a conflicting sentence, the task instructions were presented visually on half of the

trials and auditorily on the other half, followed by both letter strings and white noise. On memory recall trials, participants were instructed to keep thinking about their autobiographical memory, in as much detail as possible, until the end of the trial. Each trial was followed by a jittered fixation (1-3) and a task focus rating question. Participants were required to rate their task focus on a scale of 1 (i.e., not at all focused) to 4 (i.e., highly focused) within 2 s, using a button press to respond.

Each condition contained 24 trials; stimuli were presented across four runs, with each containing 30 trials. Each trial lasted 14.8-21.2 s with an average of 18.0 s. The whole experiment lasted 36 minutes. Trials were presented in a pseudorandom order, ensuring that trials from the same experimental condition were not presented consecutively more than twice, and the memory cue word of each trial was only presented once in each run (the memory cue word was presented a maximum of two times across the whole experiment).

Materials.

Study 1: This study included 50 paired topic sentences, which therefore resulted in two experiment versions, each containing 25 easy and 25 hard sentences. The versions were counterbalanced across participants. These sentences contained accessible factual content on non-emotive topics, with easy texts selected from BBC Bitesize and hard texts selected from Wikipedia. For example, the topic MYTH included an easy version, “Myths are ancient tales filled with magical creatures, gods and mystery that are passed down the generations and not based on facts or reality”, whereas the hard version was, “Myth is a genre of folklore or theology consisting primarily of narratives that play a fundamental role in society such as foundational tales”. The full set of stimuli used is available on OSF (https://osf.io/cqbhv/overview?view_only=ea533ec03ad3471a8336cc32107c15f6). We collected ratings for the sentences used in this study from separate cohorts of participants (i.e., individuals who did not take part in the fMRI experiment). Participants rated the difficulty (n=24), and interestingness (n=22) of the sentences on a 7-point scale, ranging from 1 (i.e., “extremely easy”; “not at all interesting”) to 7 (i.e., “extremely difficult”; “extremely interesting”). Overall, the easy sentences were rated as significantly easier to understand, more interesting, more frequent (SUBTLEX_US word frequency database; ref. Brysbaert &

New, 2009), and they contained more words than the hard sentences (Bonferroni-corrected $p < .05$). There was no difference in concreteness (ref. Brysbaert et al., 2014; all $F < .10$ for cue words). We balanced the number of characters across the easy and hard conditions (all paired t-test, Bonferroni-corrected $p > .05$), to ensure that the visual loadings were comparable across conditions.

For the arithmetic task, the easy condition consisted of additions of zeros, whereas the hard condition involved additions with random numbers between 1 and 4.

To induce a mind wandering state prior to each comprehension or arithmetic trial, we presented a cue phrase before each sentence. A total of 25 cue phrases were selected from the positive set used in ref. (Schlagman & Kvavilashvili, 2008) (e.g., “Stars at night”, “Lottery win”). The same cue phrases were used across all conditions and were counterbalanced across runs to ensure that no phrase was repeated within the same run.

Study 2: This study presented participants with 96 sentences, all of which were preceded by a cue word. The sentences were selected using 96 highly frequent and concrete nouns as key words as a search term in Wikipedia to identify text that described largely unfamiliar facts about each item (sentence length: Mean $\pm$ SD = 20.33 $\pm$ 1.54 words). These sentences contained accessible factual content, on non-emotive topics; for example, “Posters are used for reproductions of artwork, particularly famous works, and are cheaper compared to the original” for the keyword POSTER. The full set of sentences is available on OSF (https://osf.io/cqbhv/overview?view_only=ea533ec03ad3471a8336cc32107c15f6). The sentences were divided into four sets and assigned to the following conditions: (1) read sentences; (2) listen to sentences; (3) retrieve personal memories while ignoring visual sentences; (4) retrieve personal memories while ignoring auditory sentences. We collected ratings for the sentences used in this study from separate cohorts of participants (i.e., they did not take part in the fMRI experiment). Participants rated the familiarity ($n=16$), and comprehensibility ($n=20$) of the sentences, on a 7-point scale, from 1 (i.e., “completely unfamiliar”; “very hard to understand”) to 7 (i.e., “extremely familiar”; “very easy to understand”). Overall, the sentences were unfamiliar (familiarity: Mean $\pm$ SD = 4.23 $\pm$ 1.15),

easy to understand (comprehensibility: Mean $\pm$ SD = 6.12 $\pm$ 0.43) and did not differ in familiarity and comprehensibility between conditions (all $F < .38$).

Each sentence was preceded by a cue word, to induce autobiographical memory recall. These cue words were 60 highly frequent and concrete nouns. The autobiographical memory cues were repeated twice across the whole experiment. Spoken autobiographical memory cues and sentences were recorded by a male native British English speaker, using Audacity (<http://audacity.sourceforge.net/>), in a sound-attenuated room. The stimuli were normalized for volume and power in Audacity, producing a level of -3 dB FS. The MRI auditory stimulus system (MR Confon mkII+, www.mr-confon.de/en/products.html) was used to give a maximum presentation level of 80–90 dB SPL.

The key words and cue words were matched for key psycholinguistic properties across conditions: they did not differ in lexical frequency (SUBTLEX_US word frequency database; ref. Brysbaert & New, 2009) or concreteness (ref. Brysbaert et al., 2014; all $F < .10$ for cue words). In addition, there were no significant differences between the four sentence conditions in lexical frequency or concreteness for all the words contained in the sentences (all $F < 0.44$).

Analysis.

Parametric effects of task focus were decoded using the online tool Neurosynth (Yarkoni et al., 2011). Neurosynth (RRID: SCR_006798) is an automated meta-analysis tool that uses text-mining approaches to extract terms from neuroimaging articles that typically co-occur with specific peak coordinates of activation. It can be used to generate a set of terms frequently associated with a spatial map. Word clouds were generated using Python. We excluded terms referring to neuroanatomy (e.g., “inferior” or “sulcus”), and repeated terms (e.g., “semantic” and “semantics”). The size of the word in the word cloud reflects the frequency of that term across other studies, and the colour indicates its relationship with focus rating in our study (i.e., red = positive correlation with task focus, blue = negative correlation with task focus).

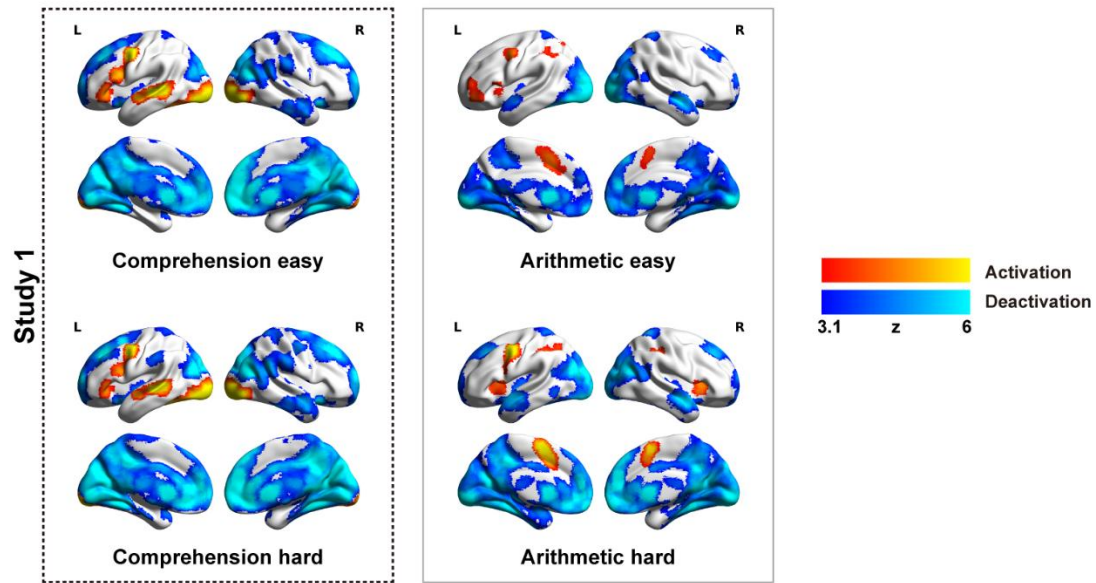


Figure S2.1 Univariate activation results for comprehension and arithmetic in study 1 ($N = 34$). Warm colours = task > implicit baseline. Cold colours = task < implicit baseline. All maps were cluster corrected at $z > 3.1, p < .05$.

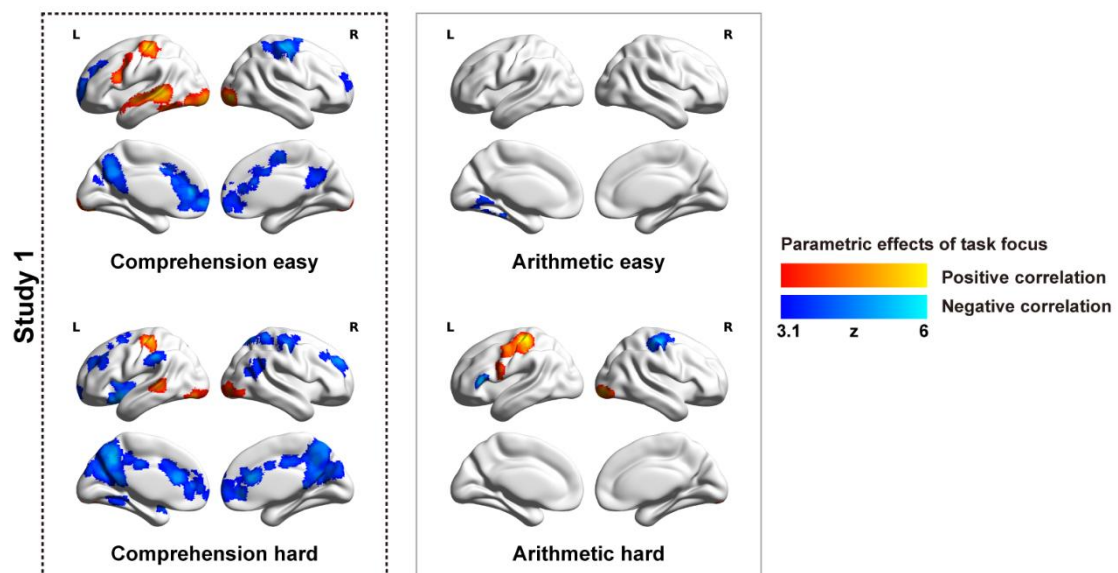


Figure S2.2 Parametric effects of task focus for easy and hard comprehension and arithmetic in study 1. In this analysis, eight Explanatory Variables (EV) of interest and four of no interest were modelled using a double-Gaussian hemodynamic response gamma function: 1. easy comprehension; 2. hard comprehension; 3. easy arithmetic; 4. hard arithmetic; 5-8.

parametric effect of focus for easy and hard comprehension and arithmetic; 9. memory cue phrase; 10. fixation before sentences or numbers; 11. fixation before the rating question; 12. rating decision period. 35 participants were recruited; one was excluded because of big head movement, and another was excluded due to a lack of variation in focus ratings during easy arithmetic task across all runs. Therefore, 33 participants were included in this group-level analysis. These brain regions show greater activation (red) or greater deactivation (blue) when participants reported higher task focus. Results were cluster corrected at $z > 3.1$, $p < .05$.

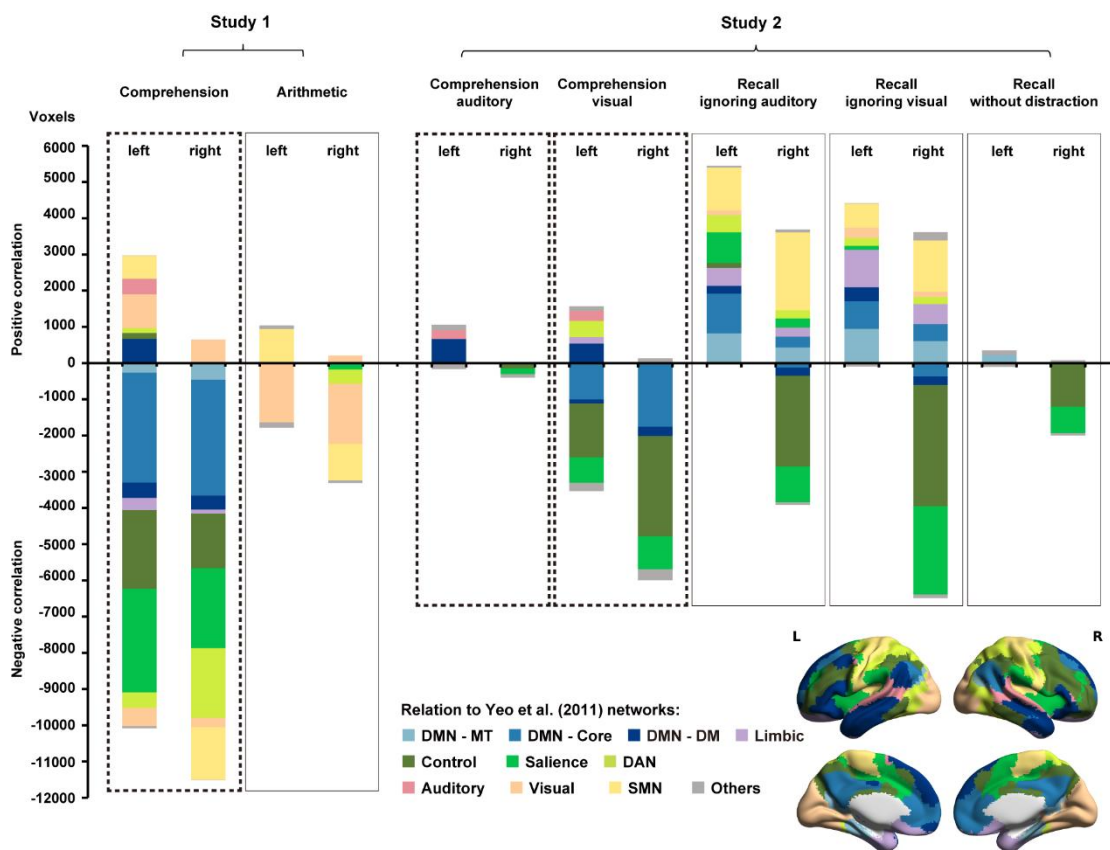


Figure S2.3 Network analysis of focus effects in Study 1 and 2. The chart shows counts of voxels per network that were significantly correlated with task focus ratings. Top: networks showing greater activation with higher task focus. Bottom: networks showing greater deactivation with higher task focus (see **Figure 2.2** and **Figure 2.3**). Networks with fewer than 100 activated/deactivated voxels were collapsed into the "Others" category. DMN,

default mode network; MT, medial temporal; DM, dorsal medial; DAN, dorsal attention network; SMN, somatomotor network.

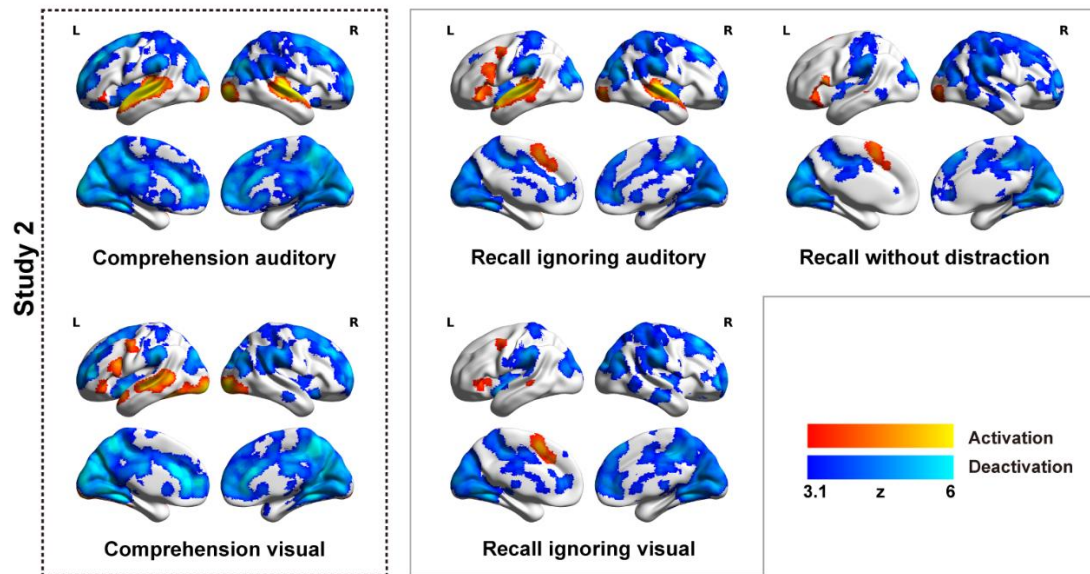


Figure S2.4 Univariate activation results for comprehension and autobiographical memory retrieval in study 2 ($N = 26$). Warm colours = task > implicit baseline. Cold colours = task < implicit baseline. All maps were cluster corrected at $z > 3.1$, $p < .05$.

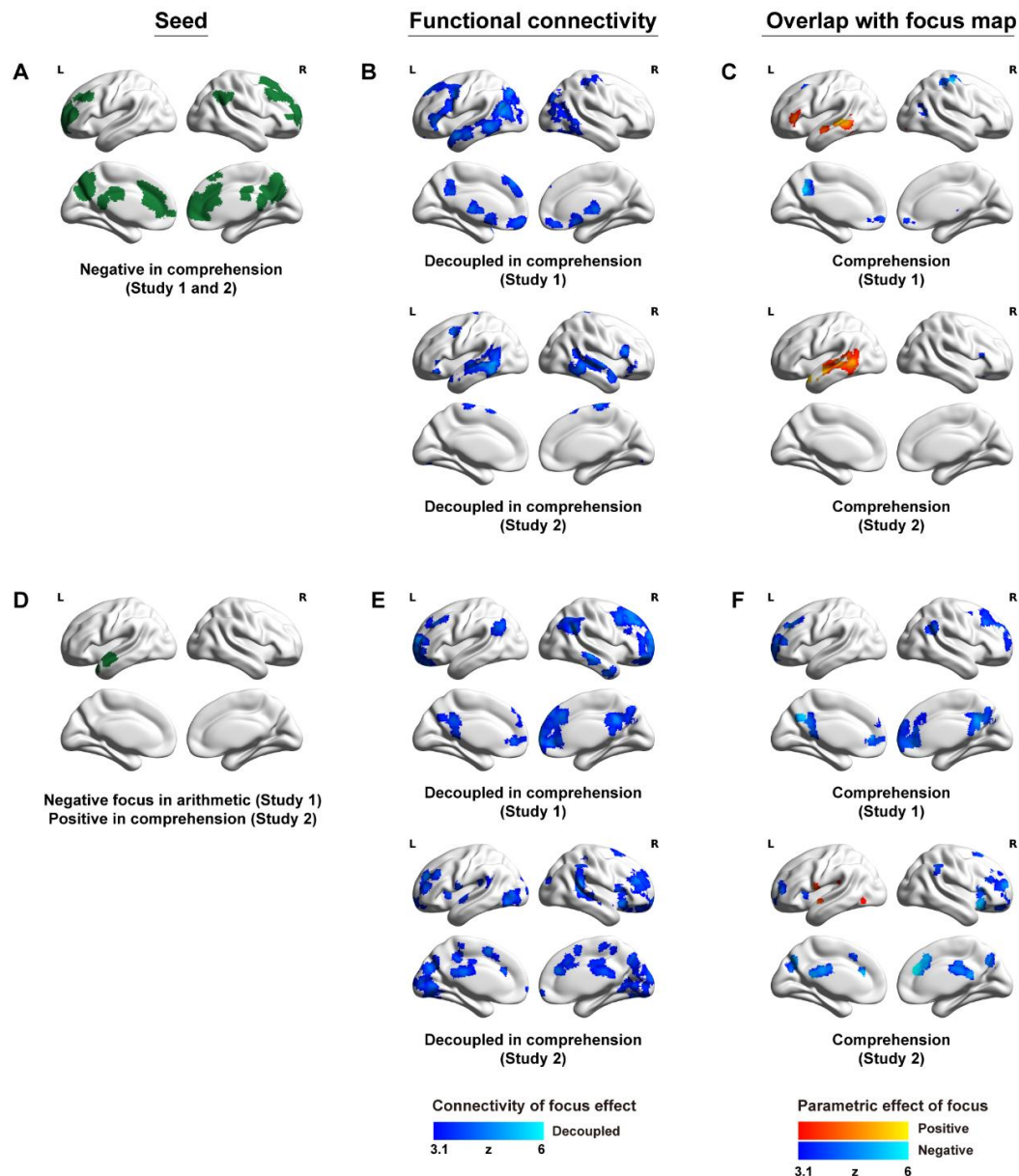


Figure S2.5 Task-based functional connectivity. (A) Seed showing greater deactivation when participants reported higher focus during comprehension across studies 1 and 2. (B) The functional connectivity maps seeded from (A). These regions (blue) showed greater decoupling from the seed when higher focus was reported during comprehension in study 1 or study 2. (C) The overlap regions obtained by masking focus maps by regions in (B), showing greater activation (red) or deactivation (blue) when greater focus was reported during comprehension. (D) Seed showing greater activation when participants reported higher focus during comprehension in study 1. (E) The functional connectivity maps seeded from (D). These regions (blue) showed greater decoupling from the seed when higher focus was

reported during comprehension. (F) The overlap regions obtained by masking the focus maps by regions in (E), showing greater deactivation (blue) when greater focus was reported during comprehension. Results were cluster corrected at $z > 3.1$, $p < .05$.

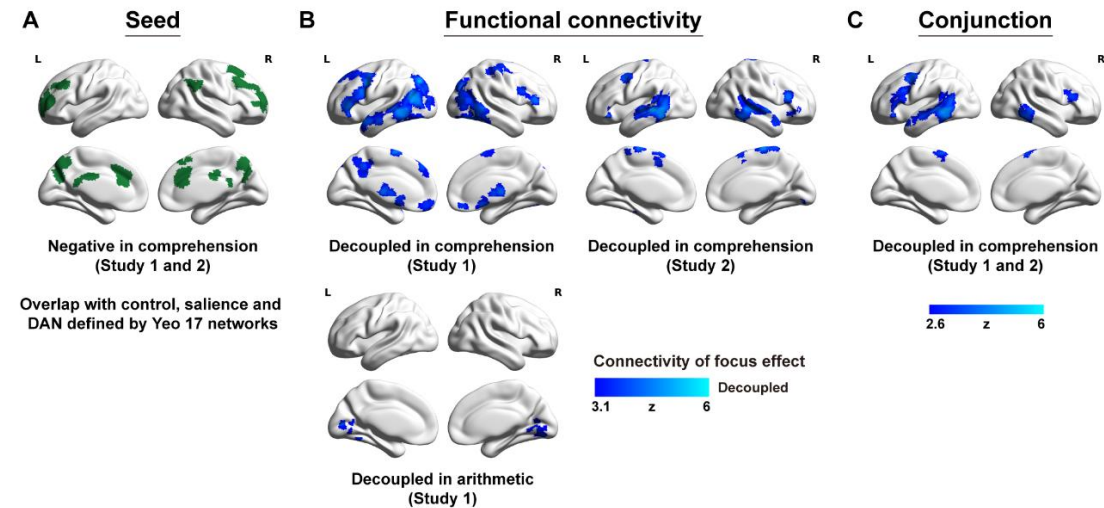


Figure S2.6 Task-based functional connectivity seeding from Control/Salience/DAN regions (A). (A) Seed region showing greater deactivation when participants reported higher focus during comprehension across studies 1 and 2. This seed was generated from the conjunction of comprehension across studies 1 and 2, masked by the control, salience, and dorsal attention (DAN) networks defined by Yeo et al. (2011). (B) Functional connectivity maps seeded from (A). These regions (blue) showed greater decoupling from the seed when higher task focus was reported. Results were cluster corrected at $z > 3.1$, $p < .05$. (C) The conjunction of PPI results during comprehension across studies 1 and 2. These regions (blue) showed greater decoupling from the seed when higher focus was reported during comprehension. The conjunction result was cluster corrected at $z > 2.6$, $p < .05$.

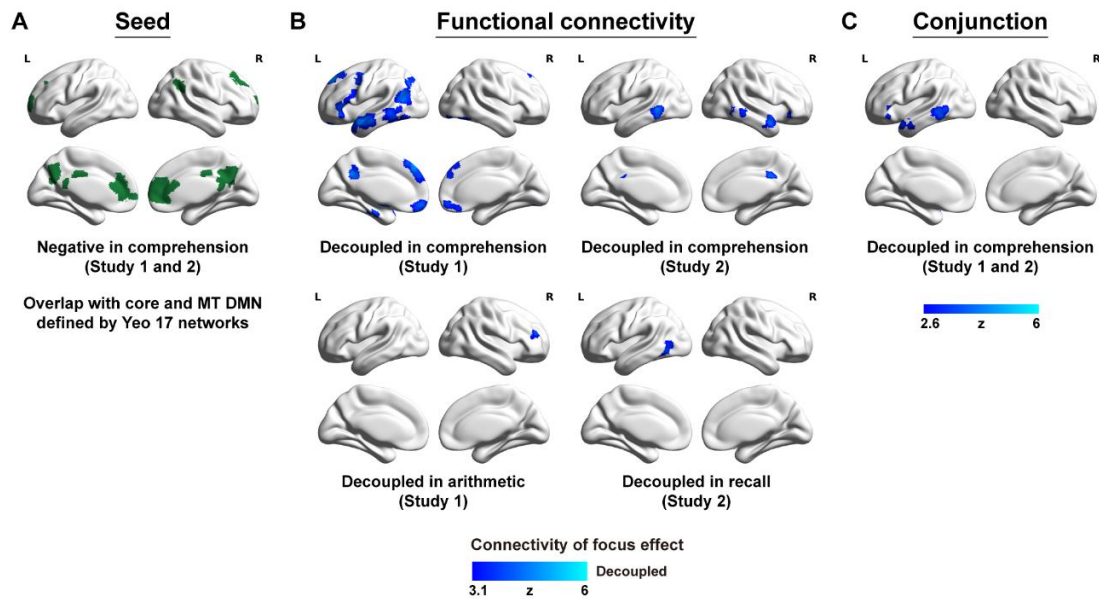


Figure S2.7 Task-based functional connectivity seeding from Core/MT DMN regions (A). (A) Seed region showing greater deactivation when participants reported higher focus during comprehension across studies 1 and 2. This seed was generated from the conjunction of comprehension across studies 1 and 2, masked by the core and medial temporal (MT) DMN defined by Yeo et al. (2011). (B) Functional connectivity maps seeded from (A). These regions (blue) showed greater decoupling from the seed when higher task focus was reported. Results were cluster corrected at $z > 3.1$, $p < .05$. (C) The conjunction of PPI results during comprehension across studies 1 and 2. These regions (blue) showed greater decoupling from the seed when higher focus was reported during comprehension. The conjunction result was cluster corrected at $z > 2.6$, $p < .05$.

Table S2.1 Study 1 linguistic properties of sentences, mean (SD).

Sentences	Word count	Character count	Difficulty	Frequency	Concreteness	Interestingness
Version 1 - comprehension - easy	21 (3)	100 (13)	1.83 (.37)	4.15 (.28)	2.76 (.23)	3.25 (.91)
Version 1 - comprehension - hard	19 (2)	103 (12)	4.22 (.68)	3.67 (.41)	2.62 (.20)	2.5 (.74)
Version 2 - comprehension - easy	22 (2)	101 (9)	1.85 (.36)	4.19 (.37)	2.73 (.18)	3.34 (.79)
Version 2 - comprehension - hard	19 (2)	104 (14)	4.43 (.76)	3.71 (.46)	2.58 (.28)	2.41 (.67)

Table S2.2 Study 2 linguistic properties of cue words and sentences, mean (SD).

Stimuli set	Frequency	Concreteness	Familiarity	Comprehensibility
(i) autobiographical memory cues	2.83 (.50)	4.73 (.29)	/	/
(ii) autobiographical memory cues	2.86 (.50)	4.69 (.43)	/	/
(iii) autobiographical memory cues	2.88 (.46)	4.75 (.30)	/	/
(iv) autobiographical memory cues	2.87 (.50)	4.72 (.39)	/	/
(v) autobiographical memory cues	2.86 (.50)	4.74 (.35)	/	/
(i) sentences - comprehension	3.21 (.22)	2.70 (.25)	4.25 (1.13)	6.18 (.34)
(ii) sentences - comprehension	3.18 (.20)	2.74 (.22)	4.32 (1.22)	6.10 (.48)
(iii) sentences - recall	3.20 (.15)	2.77 (.26)	4.03 (0.99)	6.07 (.46)
(iv) sentences - recall	3.20 (.20)	2.72 (.19)	4.31 (1.27)	6.13 (.46)

Supplementary Information for Chapter 3

Thought patterns and comprehension accuracy

To further examine how thought patterns related the comprehension of easy and hard texts within each text type, we fitted separate models for factual and story texts across difficulty levels. The best fitting GLMMs included the fixed effects of five thought components, text difficulty (easy, hard), and their interactions. Random intercepts were included for participants and items. By-item random slopes for one thought component were included in each model, again reflecting the maximal structure supported by the data.

For factual texts, accuracy was higher for easy than hard texts (Appendices, Table S3.1). In addition, higher scores on Component 1 were associated with poorer comprehension, whereas higher scores on Component 4 were associated with better comprehension, consistent with the across-text analysis. For story texts, accuracy was also higher for easy than hard texts (Appendices, Table S3.2), but no reliable associations were observed between thought patterns and comprehension.

Effect of difficulty on reading time

Forty-seven participants' reading time was recorded during the experiments. Paired t-tests were conducted to examine differences in reading time between easy and hard texts separately for each experiment. Prior to analysis, outliers in reading time were screened at the within-subject, within-condition level using a ± 2.5 SD criterion. No trials met this criterion; therefore, all analyses were conducted on the original data. For each participant, reading time were averaged across trials within each difficulty condition separately for factual and story texts. When comparing the two text types, reading time were likewise averaged across trials within each text type. Within each experiment, the distribution of difference scores in mind-wandering frequency (easy vs. hard) was approximately symmetric, and paired t-tests were used to compare mind-wandering frequency between easy and hard conditions. The same approach was applied when comparing the two text types.

The results (see Figure S3.2) showed that, for both factual text and short story comprehension, reading time was significantly longer when participants read hard texts

compared with easy texts (factual text: $t(46) = -6.75, p < .001$; short story: $t(46) = -2.39, p = .021$). When comparing the two text types, participants spent more time during factual text comprehension than during short story comprehension ($t(46) = 4.51, p < .001$).

Reading time and instances of mind-wandering

Mind-wandering instances were analysed using a generalized linear mixed model with a Poisson distribution, implemented with glmmTMB package in R version 4.4.2 (R Core Team, 2024). Sum coding ($-0.5, 0.5$) was used for categorical variables. Post hoc comparisons were conducted using the emmeans package (Lenth, 2024). The best fitting model included fixed effects of reading time, text types (factual, story), and their interaction, as well as by-participant random intercepts and random slopes for text type and reading time, and by-item random intercepts.

The result showed that longer reading time significantly predicted higher mind-wandering frequency (Appendices, Table S3.3). In addition, participants exhibited significantly more mind-wandering during factual text comprehension than during short story comprehension, consistent with the result from the paired t-test analysis comparing text types. The interaction between reading time and text type was not significant.

Reading time and comprehension accuracy

To assess whether reading time during reading predicted comprehension accuracy, we employed generalized linear mixed models (GLMMs) using the glmer function in the lme4 package. Comprehension accuracy for each text was modelled as a binomial response using the number of correct and incorrect responses with a logit link function. Sum coding ($-0.5, 0.5$) was used for categorical variables. The best fitting model included fixed effects of reading time, text types (factual, story), and their interactions, as well as by-participant and by-item random intercepts and random slopes for text type.

The result showed that accuracy was significantly higher during factual text comprehension than during short story comprehension, consistent with previous results (Appendices, Table S3.4). Reading time did not significantly predict comprehension accuracy. The interaction between reading time and text type was also not significant.

Reading time and thought patterns

To assess whether the patterns of ongoing thought during reading predicted reading time, we employed linear mixed-effects models (LMMs) using the lmer function in the lme4 package. Sum coding (−0.5, 0.5) was used for categorical variables. The best fitting model included fixed effects of five thought components, text types (factual, story), and their interactions. The model also included by-participant and by-item random intercepts and random slopes for the Component 1 and text type.

Reading time was shorter for stories than for factual texts (Table S3.5). Higher scores on the two task-unrelated components -- Component 1 (“future problem solving”) and Component 2 (“intrusive social thought”) -- were associated with longer reading time. In contrast, higher scores on Component 4 (“deliberate detail”) were associated with shorter reading time.

Task focus and Thought patterns

LMM was used to examine the relationship between the patterns of ongoing thought during reading and task focus. The best fitting model included fixed effects of five thought components, text types (factual, story), and their interactions. The model also included by-participant random intercepts and random slopes for the Component 1.

Higher scores on the Component 1 (“future problem solving”) and Component 2 (“intrusive social thought”) were significantly associated with lower task focus. In contrast, higher scores on Component 4 (“deliberate detail”) were associated with higher task focus (Table S3.6).

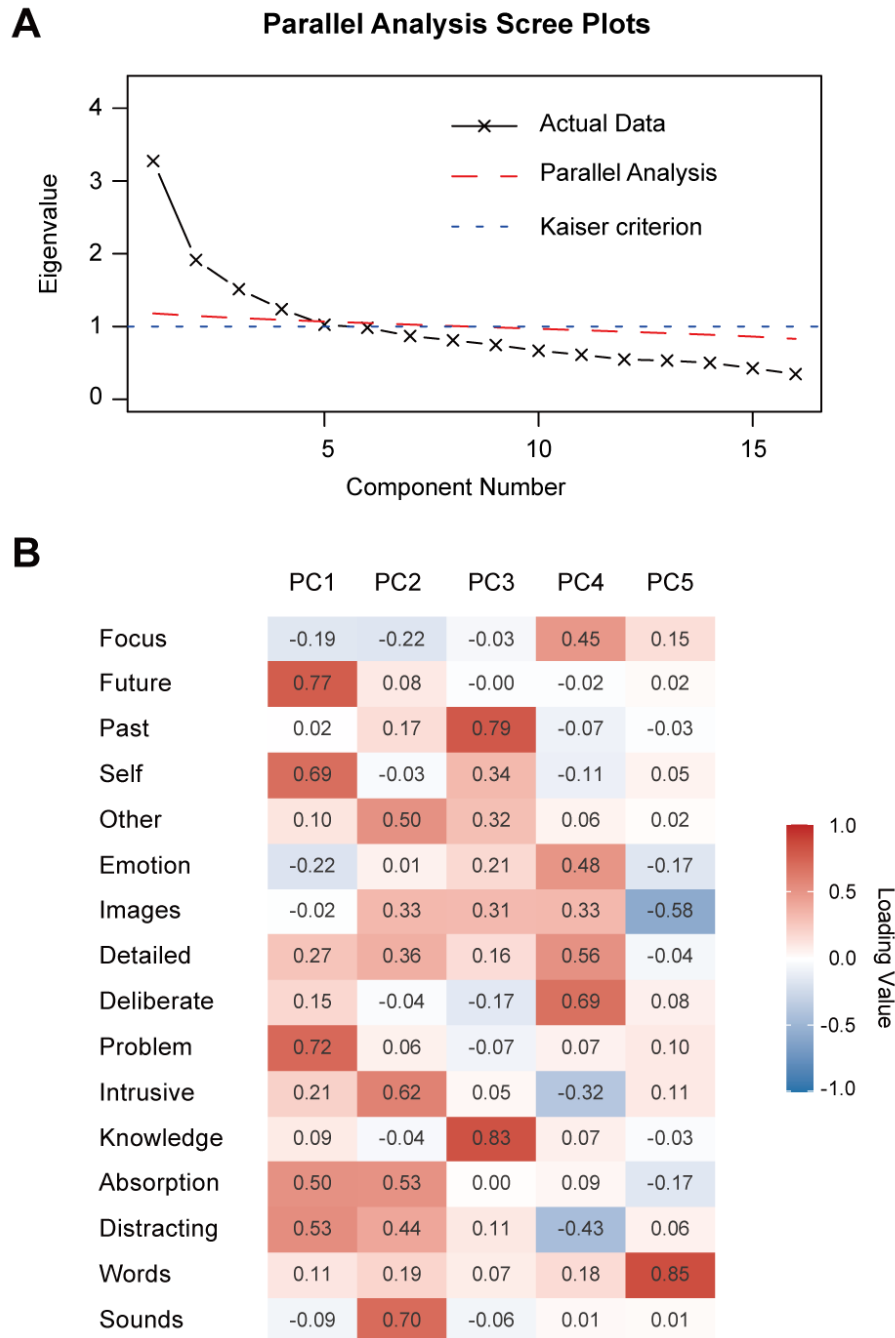


Figure S3.1 PCA analysis results. (A) Scree plot showing eigenvalues for each principal component. The solid black line with X markers represents the actual data eigenvalues. The dotted blue line marks the Kaiser criterion (eigenvalue = 1). The dashed red line shows the simulated eigenvalues from parallel analysis. (B) Heatmap of PCA loadings for five principal components identified based on eigenvalue > 1. The colour scale reflects the strength and direction of the loadings (range: -1 to +1), with cold colours indicating negative loadings and warm colours indicating positive loadings.

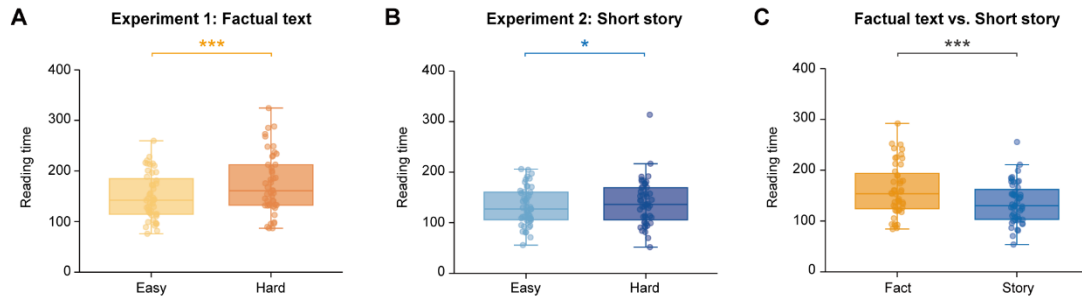


Figure S3.2 Reading time differences across text difficulty and text type. Boxplots show individual-level reading time. Panel A shows the paired t-test results comparing easy and hard texts in factual texts. Panel B shows the same comparison within story texts. Panel C shows paired t-test results comparing factual texts and short stories. The box indicates the interquartile range (IQR), the horizontal line inside the box marks the median, and the whiskers extend to the most extreme data points within 1.5 times the IQR. *** $p < .001$, * $p < .05$.

Table S3.1 Results of generalized linear mixed model predicting comprehension accuracy from thought components for factual text.

	β	SE	Z value	p
Intercept	0.88	0.14	6.50	< .001 ***
PC1	-0.29	0.06	-4.68	< .001 ***
PC2	-0.10	0.07	-1.46	0.145
PC3	0.09	0.06	1.56	0.118
PC4	0.27	0.06	4.36	< .001 ***
Difficulty	-0.67	0.11	-6.06	< .001 ***
PC1 $\times$ Difficulty	0.03	0.11	0.32	0.751
PC2 $\times$ Difficulty	0.15	0.11	1.40	0.161
PC3 $\times$ Difficulty	-0.16	0.11	-1.44	0.151
PC4 $\times$ Difficulty	0.03	0.11	0.24	0.814

Table S3.2 Results of generalized linear mixed model predicting comprehension accuracy from thought components for story text.

	β	SE	Z value	p
Intercept	1.59	0.32	4.97	< .001 ***
PC1	-0.13	0.07	-1.95	0.051
PC2	-0.12	0.08	-1.54	0.123
PC3	0.02	0.07	0.31	0.756
PC4	0.10	0.07	1.47	0.141
Difficulty	-0.49	0.12	-4.15	< .001 ***
PC1 $\times$ Difficulty	0.14	0.12	1.13	0.260
PC2 $\times$ Difficulty	-0.02	0.12	-0.14	0.888
PC3 $\times$ Difficulty	0.05	0.12	0.36	0.717
PC4 $\times$ Difficulty	-0.06	0.12	-0.47	0.642

Table S3.3 Results of generalized linear mixed model predicting mind-wandering frequency from reading time.

	β	SE	Z value	p
Intercept	1.34	0.09	14.37	< .001 ***
Reading time	0.25	0.04	6.15	< .001 ***
Text type	-0.32	0.08	-3.78	< .001 ***
Reading time $\times$ Text type	0.01	0.05	0.11	0.915

Table S3.4 Results of generalized linear mixed model predicting comprehension accuracy from reading time.

	β	SE	Z value	p
Intercept	1.40	0.20	7.13	< .001 ***
Reading time	0.10	0.09	1.17	0.243
Text type	0.83	0.38	2.21	0.028 *
Reading time $\times$ Text type	0.22	0.17	1.35	0.178

Table S3.5 Results of linear mixed model predicting reading time from thought components for all texts.

	β	SE	Z value	p
Intercept	150.33	6.57	22.88	< .001 ***
PC1	6.60	1.85	3.57	0.001 **
PC2	6.51	1.46	4.45	< .001 ***
PC3	0.69	1.27	0.54	0.588
PC4	-2.74	1.37	-1.99	0.047 *
Task	-20.93	6.48	-3.23	0.002 **
PC1 $\times$ Task	-3.09	3.00	-1.03	0.315
PC2 $\times$ Task	0.18	2.81	0.06	0.950
PC3 $\times$ Task	-0.99	2.49	-0.40	0.691
PC4 $\times$ Task	3.66	2.68	1.37	0.172

Table S3.6 Results of linear mixed model predicting task focus from thought components for all texts.

	β	SE	Z value	p
Intercept	6.07	0.13	46.09	< .001 ***
PC1	-0.51	0.10	-5.10	< .001 ***
PC2	-0.63	0.06	-10.66	< .001 ***
PC3	-0.09	0.06	-1.58	0.114
PC4	1.12	0.06	19.43	< .001 ***
Task	0.12	0.10	1.25	0.210
PC1 $\times$ Task	0.02	0.10	0.17	0.867
PC2 $\times$ Task	0.01	0.10	0.13	0.894
PC3 $\times$ Task	0.13	0.10	1.27	0.204
PC4 $\times$ Task	-0.08	0.10	-0.77	0.439

Supplementary Information for Chapter 4

Network analyses: To further examine the variability within networks in the Schaefer 7 network atlas, we extracted the pRFs R^2 based on the Schaefer 400 parcels, 17 network atlas. We reorganized the 17 networks into eight functional networks. Each subnetwork from the 17-network atlas was mapped to its corresponding network defined in the 7-network atlas, to maintain consistency with the functional organization. The only exception was the Temporal Parietal subnetwork, which we treated as an independent network due to its different function from the DMN subsystems. As a result, the following 8-network structure was defined: Visual network – Visual A, Visual B; Somatomotor network – Somatomotor A, Somatomotor B; Dorsal attention network (DAN) – DAN A, DAN B; Ventral attention network (VAN) – VAN A, VAN B; Control network – Control A, Control B, Control C; Default network - Default A, Default B, Default C; Limbic network – Limbic A, Limbic B; Temporal Parietal network. Before the analysis, we removed 1% of the pRFs R^2 that fell outside the mean ± 3 standard deviations (SD) for each parcel.

We employed Linear Mixed-effects Models for each of the eight functional networks. For the first seven networks, each model included fixed effects of subnetworks, hemisphere, pRFs, and their interaction, with adjustments for random intercepts for participants and parcels, as well as by-participant random slopes for of subnetworks, hemisphere and pRFs, and by-parcel random slopes for pRFs. An exception was the model for the Limbic network, where the model structure excluded by-parcel random slopes for pRFs. For the Temporal-Parietal network, the model included fixed effects of hemisphere, pRFs, and their interaction, with adjustments for random intercepts for participants and parcels, as well as by-participant random slopes for hemisphere and pRFs. The dependent variable was R^2 value associated with each combination of network, hemisphere and pRFs. P-values were Bonferroni-corrected to control multiple comparisons. All results were shown in Table S4.4.

The visual network showed a significant main effect of subnetwork, pRFs and their interaction (all corrected $p < .001$), indicating the difference of the distribution of pRFs in Visual subnetworks. The post hoc revealed that in both Visual A and B subnetworks, +pRFs showed significantly higher R^2 than -pRFs, though the effect sizes differed (Visual A: $\beta =$

0.113, $p < .001$; Visual B: $\beta = 0.022$, $p = .030$). The DAN also showed a significant main effect of subnetwork, pRFs and their interaction (all corrected $p < .001$). The further analysis revealed that for DAN A, +pRFs exhibited significantly higher R^2 than -pRFs ($\beta = 0.037$, $p < .001$). For DAN B, this difference was smaller but still statistically significant, with +pRFs showing higher R^2 than -pRFs ($\beta = 0.015$, $p = 0.004$). In contrast, there was a significant interaction between subnetwork and pRFs in Limbic network. The post hoc analysis showed that in Limbic B, -pRFs exhibited significantly higher R^2 than +pRFs ($\beta = -0.003$, $p < .001$), whereas no significant difference was observed in Limbic A.

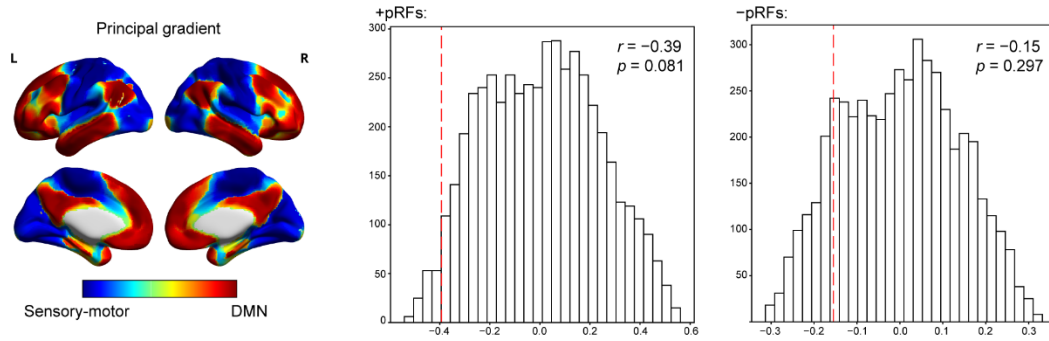


Figure S4.1 Statistical significance of correlations between positive/negative retinotopic coding maps and the principal gradient was assessed using the spin permutation test (5000 permutations). The left map presents the principal gradient from Margulies et al. (2016).

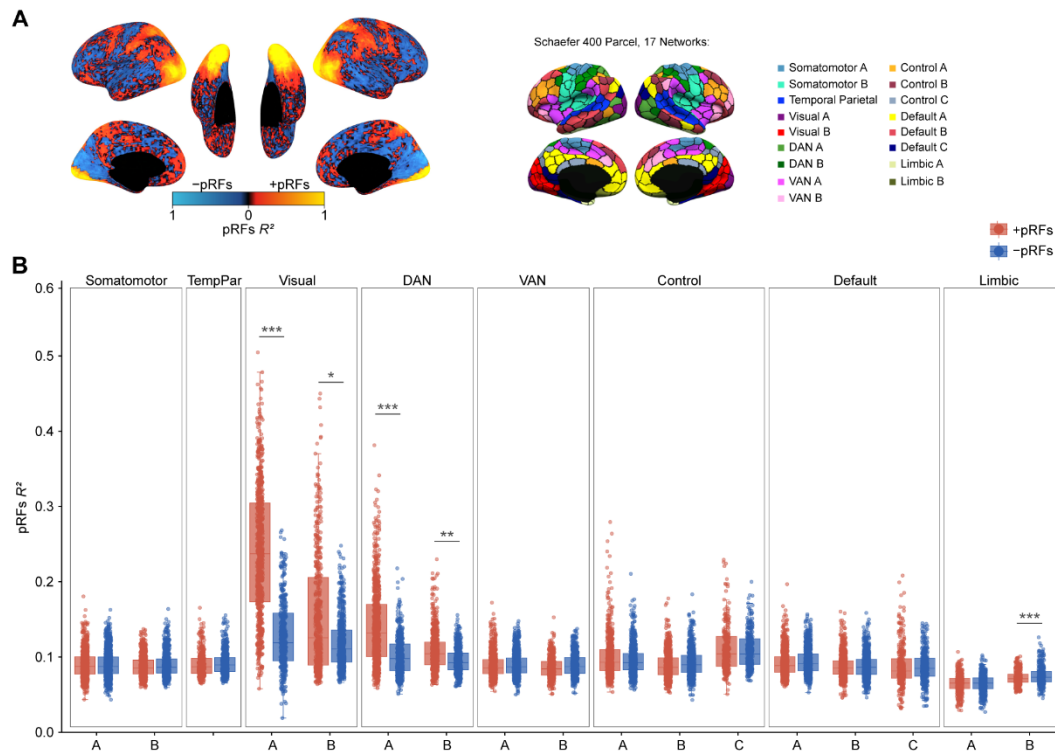


Figure S4.2 Positive and negative pRFs throughout the cortex. (A) The is on inflated lateral, ventral, and medial views depict the coefficient of determination of the pRF model prediction (pRF R^2) multiplied by the sign of the estimated amplitude parameter (color scale: +pRFs: red colours; -pRFs: blue colours), for the averaged time series across the participants. The lower map presents the 400 parcel parcellation matched to Yeo 17 network parcellation from Schaefer et al. (2018). (B) The boxplots show the individual parcel-level R^2 of positive and

negative pRFs in 17 networks defined in Schaefer et al. (2018). The colours represent the type of pRFs (warm: +pRFs; cold: -pRFs). The box indicates the interquartile range (IQR), the horizontal line inside the box marks the median, and the whiskers extend to the most extreme data points within 1.5 times the IQR. Statistical comparisons are based on the linear mixed-effects models (see Table S4.4). *** $p < .001$, ** $p < .01$, * $p < .05$.

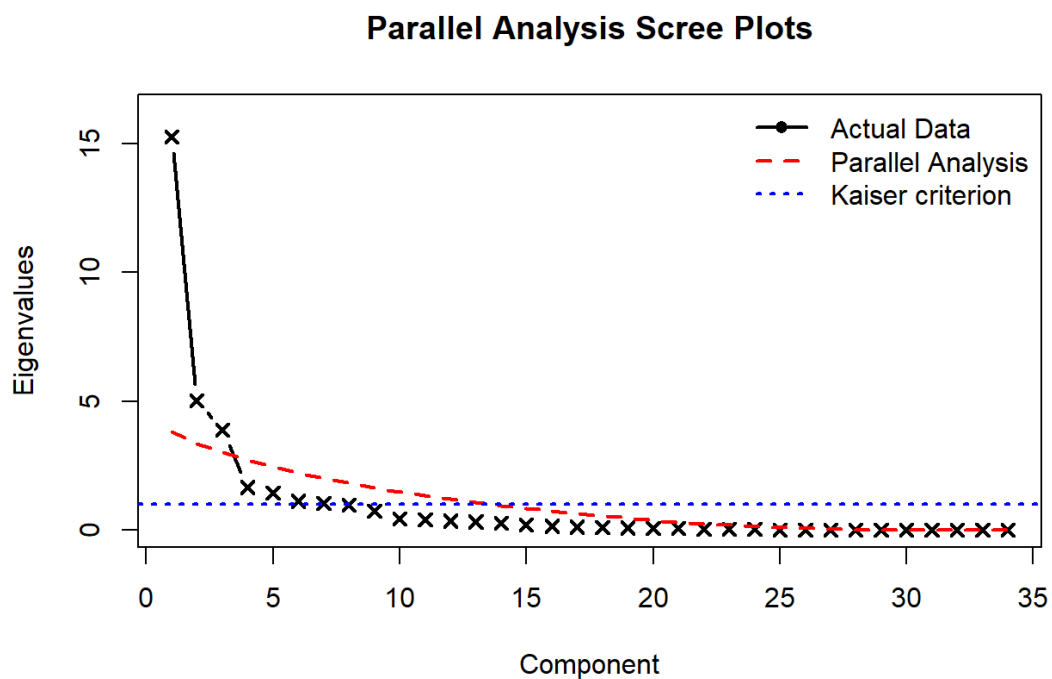


Figure S4.3 Scree plot showing eigenvalues for each principal component. The dotted blue line marks the Kaiser criterion (eigenvalue = 1).

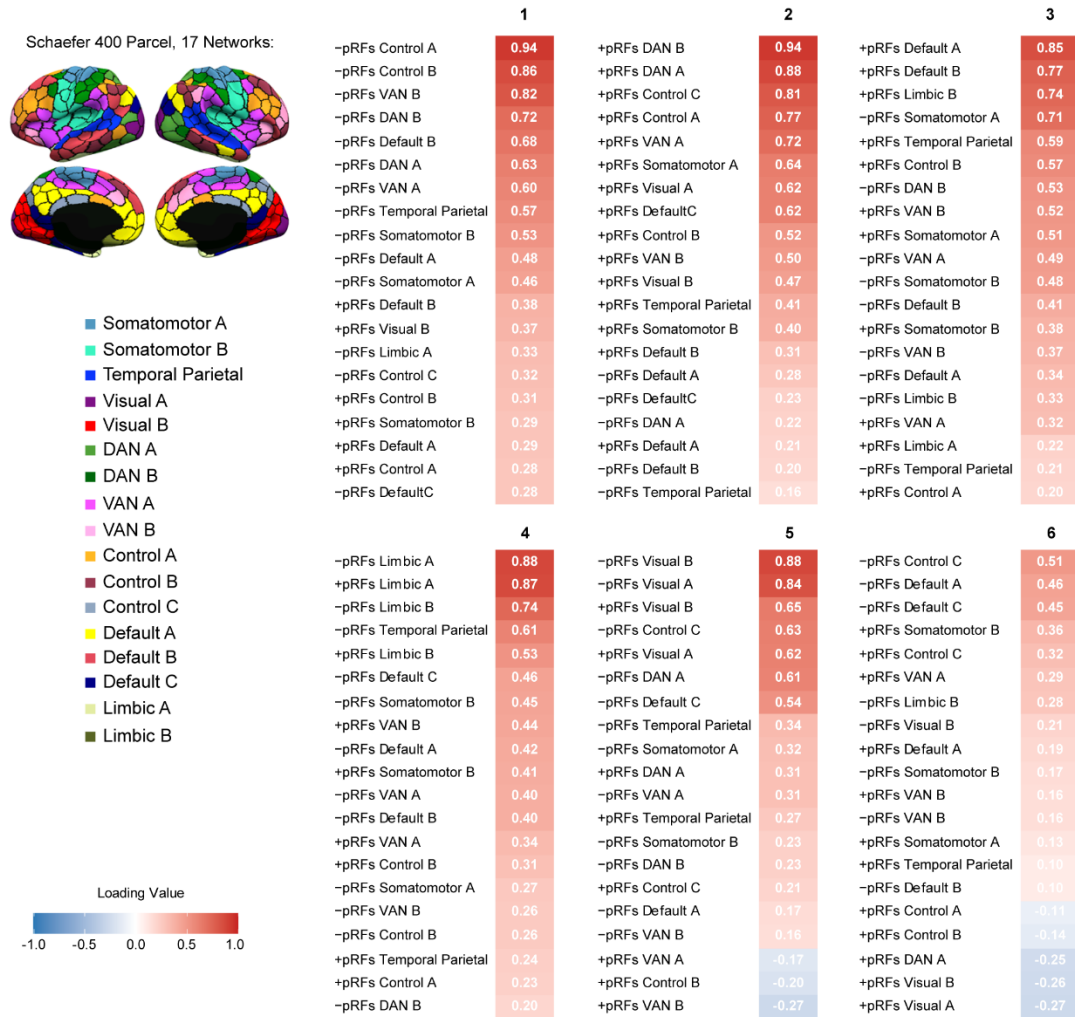


Figure S4.4 Heatmap of PCA loadings for principal components 1-6 identified in our analysis. The top 20 variables with highest absolute loading values are shown. The size of the word in the word cloud reflects the strength of the loadings, and the colour indicates the direction of the loadings (i.e., red = positive loadings, blue = negative loadings).

Table S4.1. Summary of the linear mixed-effects model for the pRFs R^2 across network, hemisphere and pRFs.

Predictor	NumDF	DenDF	<i>F</i> value	<i>Pr(>F)</i>
Network	6	385	66.885	< .001 ***
pRFs	1	66	25.225	< .001 ***
Hemisphere	1	403	0.304	0.582
Network $\times$ pRFs	6	386	55.379	< .001 ***
Network $\times$ Hemisphere	6	385	0.142	0.991
pRFs $\times$ Hemisphere	1	386	0.178	0.674
Network $\times$ pRFs $\times$ Hemisphere	6	386	0.183	0.982

Table S4.2 Pairwise comparisons of +pRFs vs. -pRFs within each network (Bonferroni-corrected).

Network	Estimate	SE	<i>z</i> value	<i>Corrected p</i>
Somatomotor	0.000	0.003	-0.129	1.000
Visual	0.060	0.004	17.061	< .001 ***
DAN	0.020	0.004	5.199	< .001 ***
VAN	-0.001	0.004	-0.331	1.000
Control	-0.001	0.004	-0.283	1.000
Default	-0.002	0.003	-0.578	1.000
Limbic	-0.001	0.005	-0.262	1.000

Table S4.3 ANOVA results for pRFs R^2 comparing adjacent networks by pRFs (Network $\times$ pRFs interaction).

Contrasts	Predictor	NumDF	DenDF	<i>F</i> value	Corrected <i>p</i>
Somatomotor vs. Visual	Network	1.00	135.99	101.34	< .001 ***
	pRFs	1.00	126.07	51.19	< .001 ***
	Network $\times$ pRFs	1.00	135.96	79.65	< .001 ***
Visual vs. Dors	Network	1.00	105.00	26.64	< .001 ***
	pRFs	1.00	101.16	49.11	< .001 ***
	Network $\times$ pRFs	1.00	104.98	19.75	< .001 ***
DAN vs. VAN	Network	1.00	90.99	58.07	< .001 ***
	pRFs	1.00	35.92	13.79	< .001 ***
	Network $\times$ pRFs	1.00	90.98	108.75	< .001 ***
DAN vs. Control	Network	1.00	96.00	22.48	< .001 ***
	pRFs	1.00	34.66	11.71	0.014 *
	Network $\times$ pRFs	1.00	96.00	108.23	< .001 ***
DAN vs. Default	Network	1.00	134.98	79.54	< .001 ***
	pRFs	1.00	37.26	28.75	< .001 ***
	Network $\times$ pRFs	1.00	134.91	212.07	< .001 ***
VAN vs. Control	Network	1.00	97.01	5.33	0.207
	pRFs	1.00	33.26	0.55	4.187
	Network $\times$ pRFs	1.00	97.22	0.00	8.807
VAN vs. Default	Network	1.00	135.97	0.46	4.477
	pRFs	1.00	32.92	1.66	1.861
	Network $\times$ pRFs	1.00	135.72	0.15	6.284
Control vs. Default	Network	1.00	141.00	5.20	0.216
	pRFs	1.00	31.95	1.12	2.672
	Network $\times$ pRFs	1.00	141.17	0.13	6.466
Default vs. Limbic	Network	1.00	114.97	159.70	< .001 ***
	pRFs	1.00	33.53	1.65	1.869
	Network $\times$ pRFs	1.00	114.22	0.16	6.203

Table S4.4 Summary of linear mixed-effects model results for pRF R^2 across subnetworks, hemisphere, and pRF type, for each functional network.

Network	Predictor	NumDF	DenDF	<i>F</i> value	Corrected <i>p</i>
Somatomotor:	Subnetwork	1	78	0.396	4.249
	pRFs	1	31	0.486	3.928
	Hemi	1	82	0.001	7.809
	Subnetwork $\times$ pRFs	1	66	0.655	3.370
	Subnetwork $\times$ Hemi	1	66	2.446	0.981
	pRFs $\times$ Hemi	1	66	2.752	0.815
	Subnetwork $\times$ pRFs $\times$ Hemi	1	66	1.039	2.494
Temporal Parietal:	pRFs	1	29	1.952	1.385
	Hemi	1	16	0.002	7.716
	pRFs $\times$ Hemi	1	819	0.024	7.023
Visual:	Subnetwork	1	51	18.328	< .001 ***
	pRFs	1	66	78.876	< .001 ***
	Hemi	1	44	0.029	6.931
	Subnetwork $\times$ pRFs	1	43	53.983	< .001 ***
	Subnetwork $\times$ Hemi	1	43	0.247	4.973
	pRFs $\times$ Hemi	1	43	0.052	6.562
	Subnetwork $\times$ pRFs $\times$ Hemi	1	43	0.119	5.857
DAN:	Subnetwork	1	66	15.979	0.001 **
	pRFs	1	45	35.171	< .001 ***
	Hemi	1	54	1.011	2.553
	Subnetwork $\times$ pRFs	1	48	23.365	< .001 ***
	Subnetwork $\times$ Hemi	1	48	0.419	4.163
	pRFs $\times$ Hemi	1	48	3.288	0.609
	Subnetwork $\times$ pRFs $\times$ Hemi	1	48	0.491	3.894
VAN:	Subnetwork	1	52	0.314	4.623
	pRFs	1	36	2.243	1.143
	Hemi	1	54	1.437	1.887
	Subnetwork $\times$ pRFs	1	47	5.018	0.239
	Subnetwork $\times$ Hemi	1	47	0.929	2.720
	pRFs $\times$ Hemi	1	47	0.064	6.418
	Subnetwork $\times$ pRFs $\times$ Hemi	1	47	1.885	1.411

Control:	Subnetwork	2	67	3.695	0.241
	pRFs	1	40	0.098	6.052
	Hemi	1	62	0.000	7.884
	Subnetwork $\times$ pRFs	2	55	3.470	0.305
	Subnetwork $\times$ Hemi	2	55	0.008	7.933
	pRFs $\times$ Hemi	1	55	0.559	3.664
	Subnetwork $\times$ pRFs $\times$ Hemi	2	55	0.149	6.897
Default:	Subnetwork	2	89	2.390	0.780
	pRFs	1	35	0.976	2.640
	Hemi	1	83	0.238	5.016
	Subnetwork $\times$ pRFs	2	73	1.104	2.696
	Subnetwork $\times$ Hemi	2	73	0.546	4.655
	pRFs $\times$ Hemi	1	73	0.087	6.156
	Subnetwork $\times$ pRFs $\times$ Hemi	2	73	4.384	0.128
Limbic:	Subnetwork	1	25	8.591	0.057
	pRFs	1	28	7.936	0.070
	Hemi	1	21	0.033	6.857
	Subnetwork $\times$ pRFs	1	1241	7.775	0.043 *
	Subnetwork $\times$ Hemi	1	20	0.008	7.425
	pRFs $\times$ Hemi	1	1241	0.009	7.411
	Subnetwork $\times$ pRFs $\times$ Hemi	1	1241	2.618	0.847

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