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Distinct default mode network subsystems show similarities and differences in the effect of task focus across reading and autobiographical memory

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Brief running title: Distinct roles of default subsystems in internally- and externally-oriented cognition

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Abstract

Semantic cognition can be both perceptually-coupled, for example, during reading, and decoupled, such as in daydreams. Mind-wandering, characterised by autobiographical memory retrieval, often interferes with externally-focussed tasks. This study investigated the neural basis of these states, when they occur in isolation and in competition, using fMRI. Participants were asked to read sentences, presented word-by-word, or to recall personal memories, as a proxy for mind-wandering. Task conflict was created by presenting sentences during memory recall, or memory cues before sentences. We found that different subsystems of the default mode network (DMN) do not fully dissociate across internally- and externally-oriented states, and they do not fully separate in terms of the effects of task focus; this depends on the task. The lateral temporal DMN subsystem, associated with semantic cognition, was activated across both tasks, and by sentence inputs even when they were task-irrelevant. In the core DMN subsystem, greater task focus corresponded to a selective pattern of activation during memory recall and deactivation during reading. Both DMN subsystems formed different patterns of functional coupling depending on the task. In this way, DMN supports both access to meaning from perceptual inputs and focussed internal cognitive states in the face of distracting external information.

Keywords: default mode network; functional connectivity; internally generated thoughts; semantic cognition; task focus.

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1. Introduction

Cognition not only enables us to make sense of the external world (Patterson et al. 2007; Lambon Ralph et al. 2017), it also supports internal thoughts that are independent from the surrounding environment (Svoboda et al. 2006; Smallwood and Schooler 2015; Zhang et al. 2019). These perceptually-decoupled aspects of cognition are traditionally associated with the default mode network (DMN), which tends to deactivate when participants engage in demanding externally-presented tasks (Raichle et al. 2001). This deactivation led to the initial characterisation of the DMN as "task-negative" (e.g., Raichle *et al.* 2001; Fox et al. 2005), but it is now clear that the DMN supports internally-focussed cognitive states – for example, thinking about the past, future, ourselves or other people (Christoff et al. 2009; Spreng et al. 2009; Spreng and Grady 2010; Konu et al. 2020) – both when these states occur spontaneously, during mind-wandering (Mason et al. 2007; Fox et al. 2015; Smallwood et al. 2016), and in tasks such as autobiographical memory retrieval (Spreng *et al.* 2009; Spreng and Grady 2010; Sheldon et al. 2016). Mounting evidence shows DMN can also support externally-oriented states (e.g., Wirth et al. 2011; Vatansever et al. 2015; Krieger-Redwood et al. 2016; Murphy et al. 2018), particularly in situations when we extract meaning from perceptual inputs, such as reading (Smallwood et al. 2013; Zhang *et al.* 2019). This raises questions about how DMN supports diverse perceptually-coupled and decoupled states, and what happens when these are in conflict; for example, when we are reading but become distracted by internally oriented thoughts. In these circumstances, does greater task focus on reading activate or deactivate DMN?

Recent research has proposed that internal cognitive states and externally oriented semantic tasks might activate distinct functional subdivisions within DMN (Andrews-Hanna et al. 2010; Chiou et al. 2020). Patterns of intrinsic connectivity within DMN point to separable subsystems (Andrews-Hanna *et al.* 2010; Yeo et al. 2011), focussed on (i) regions of lateral temporal cortex and anterior frontal gyrus, implicated in the representation and retrieval of conceptual knowledge (e.g., Badre and Wagner 2002; Jackson et al. 2016; Lambon Ralph *et al.* 2017), henceforth referred to as the "lateral temporal subsystem" here; (ii) medial temporal regions, such as hippocampus, that are important for episodic memory (Nyberg, McIntosh, et al. 1996; Steinvorth et al. 2005), termed as the "medial temporal subsystem"; and (iii) a "core" DMN subsystem drawing on posterior cingulate cortex, medial prefrontal cortex, and angular gyrus

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(AG), which might allow information to be transferred between these subsystems (Andrews-Hanna *et al.* 2010; Andrews-Hanna, Smallwood, et al. 2014) and which might correspond to interdigitated connectivity patterns to lateral and medial temporal subsystems (Braga and Buckner 2017; Braga et al. 2019). A functional dissociation across DMN subsystems was reported by Chiou *et al.* (2020) who found the lateral temporal DMN subsystem prefers mental activities "*interfacing with*" perceptible events, while the core DMN prefers activities "*detached from*" perceptible events. Therefore, in the case of semantic cognition, it may be that the lateral temporal subsystem supports semantic tasks (as ATL within this subsystem, for example, is often activated by semantic content but deactivated by non-semantic tasks), while the core DMN subsystem may be disengaged by perceptually coupled semantic processing (e.g., core DMN areas in AG are consistently deactivated by semantic tasks, although may still show greater deactivation for non-semantic tasks) (Humphreys et al. 2015).

An alternative possibility is that *both internal* and *external* semantically-involved mental states access common semantic processes within DMN. Meta-analyses of semantic tasks compared with non-semantic tasks have identified a distributed network that partially overlaps with DMN, particularly in ventrolateral anterior temporal lobes (ATL) within the lateral temporal subsystem, and in left AG (Binder et al. 2009; Lambon Ralph *et al.* 2017). These DMN regions typically show stronger responses during more "automatic" semantic retrieval, such as the retrieval of strong associations or dominant features (Humphreys and Lambon Ralph 2014; Davey et al. 2015; Hoffman et al. 2015; Teige et al. 2018; Teige et al. 2019). However, DMN regions also participate in controlled aspects of semantic cognition, showing stronger recruitment in demanding working memory tasks that involve decisions about meaningful objects as opposed to colour patches (Murphy *et al.* 2018), and increasing their connectivity to regions of executive cortex during challenging semantic conditions that involve the control of distracting information (Krieger-Redwood *et al.* 2016). Moreover, conceptual knowledge is implicated in both reading comprehension (Spitsyna et al. 2006; Dehaene et al. 2015) and autobiographical memory (Graham et al. 2003; Svoboda *et al.* 2006). Distinct patterns of functional connectivity from the same semantically-relevant DMN sites might therefore support these diverse states – with stronger coupling to visual cortex when we access conceptual information from external inputs – and stronger connectivity to other DMN regions when the focus is on internal cognitive states. In line with this proposal, lateral temporal DMN

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regions can form strong intrinsic connectivity with both visual regions and other DMN nodes (Murphy et al. 2017; Zhang *et al.* 2019). In addition, poor external engagement is linked to strong functional coupling between the lateral temporal and medial temporal DMN subsystems (Poerio et al. 2017).

By this view, there are key similarities within DMN between internally-focussed states and externally-oriented semantic tasks. Both require patterns of cognition that are at least somewhat removed from the activation unfolding within sensorimotor cortex. According to the "graded hub and spoke" model of semantic representation (Lambon Ralph *et al.* 2017), concepts are formed within a heteromodal semantic hub in ventrolateral ATL that is equidistant from features in sensory-motor cortex ("spokes"). This allows the extraction of "deep" heteromodal similarity patterns not present within individual sensory-motor features: for example, BANANA is conceptually related to LETTUCE, even though colour features have stronger similarity with CANARY, while shape features suggest a likeness with BOOMERANG (Patterson *et al.* 2007; Lambon Ralph et al. 2010). Fully heteromodal concepts are thought to be processed within brain regions relatively far (and therefore insulated) from spokes, such as ventrolateral ATL (Patterson *et al.* 2007; Binney et al. 2010; Visser et al. 2010; Murphy *et al.* 2017) and left AG (Price et al. 2015; Price et al. 2016; Lanzoni et al. 2020), within DMN. This proposal is consistent with insights from decompositions of whole-brain intrinsic connectivity into "gradients", which capture components of the brain's functional architecture. The "principal gradient", explaining the most variance in intrinsic connectivity, reflects the distinction between unimodal cortex and heteromodal DMN, and is also correlated with geodesic distance from primary sensorimotor landmarks on the cortical surface (Margulies et al. 2016; Vidaurre et al. 2017). Along with semantic cognition, this separation of DMN from sensorimotor cortex might be necessary for the maintenance of cognitive states that are independent from the external environment; for example, when thinking about a past or future holiday. The anatomical location of DMN at a maximum distance from sensorimotor cortex might therefore explain the contribution of regions within DMN to both semantic and perceptually-decoupled cognition.

Here, we provide a novel characterisation of the responsiveness of lateral temporal and core DMN subsystems to an externally-oriented task (reading comprehension) and an internally-oriented state (autobiographical memory recall), considering the effects of task focus when these cognitive states are in competition. Participants were asked to either comprehend sentences presented word-by-word, or recall

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personal memories. We also characterised how responses in these subnetworks are modulated by fluctuating task focus, presenting irrelevant sentences on autobiographical memory trials, and irrelevant autobiographical memory cues on reading trials, and collecting ratings of the extent to which participants were able to focus on the primary task. In this way, irrelevant autobiographical memory cues were used to elicit the kinds of cognitive states that occur when our minds wander during reading. We tested for common task activation across the DMN subsystems, given that both reading and autobiographical memory involve access to conceptual knowledge. Analyses of functional connectivity explored how semantic DMN regions might support both perceptually-coupled and decoupled mental states. The task structure also allowed us to determine if meaningful visual inputs or memory cues activate DMN regions even when task-irrelevant, and whether DMN regions always deactivate when people are more focussed on a task (or whether these patterns vary across task states and/or DMN subsystems). To anticipate, we establish that DMN subsystems do not fully dissociate across internally- and externally-oriented states, although this dimension is relevant to their functional organisation. In addition, they do not fully separate in terms of effects of task focus; this depends on the task. Instead, DMN is organised in a way that supports both access to meaning from perceptual inputs and focussed internal cognitive states in the face of distracting external information.

2. Methods

2.1. Design

Participants completed two tasks involving semantic retrieval: autobiographical memory and word-by-word reading comprehension. We employed a within-subjects 2x2 design manipulating task (Autobiographical recall vs. Reading) and conflict (Conflict vs. No conflict). In conflict trials, the two processes (Reading vs. Autobiographical recall) were pitted against one another – with participants required to either (1) recall autobiographical information, whilst words were presented one by one on the screen or (2) read a sentence while trying to suppress a cued autobiographical memory. No conflict trials were manipulated by replacing sentences and autobiographical memory cue with “XXX” strings, therefore presenting no conflicting information for participants to process.

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The experiment took place over two days. On Day 1, participants were asked to identify specific personal events linked to each autobiographical memory cue (words like PARTY). On Day 2, they recalled these memories when presented with the cue word in the scanner, and also completed the reading task, which involved reading factual sentences about similar concepts.

2.2. Participants

Twenty-nine undergraduate students were recruited for this study (age-range 18-23 years, mean age ± SD = 20.14 ± 1.26 years, 6 males). All were right-handed native English speakers, and had normal or corrected-to-normal vision. None had any history of neurological impairment, diagnosis of learning difficulty or psychiatric illness. All provided written informed consent prior to taking part and received monetary/course credits compensation for their time. Ethical approval was obtained from the Research Ethics Committees of the Department of Psychology and York Neuroimaging Centre, University of York.

2.3. Materials

One hundred and forty-four highly imageable, frequent and concrete nouns were selected to serve as key words within sentences and as cue words for autobiographical memory recall. These nouns were divided into two lists (i.e., seventy-two words for each task) that did not differ in terms of frequency ($F(1,71) = 2.85$, $p = .10$, $\eta_p^2 = .04$), imageability ($F(1,71) = .02$, $p = .88$, $\eta_p^2 < .001$), and concreteness ($F(1,71) = .09$, $p = .76$, $\eta_p^2 = .001$). The sentences were constructed by using the key words as a search term in Wikipedia to identify text that described largely unfamiliar facts about each item (Sentence Length: *Mean* ± *SD* = 20.04 ± .93 words). These sentences and the autobiographical memory cues were then divided into three sets and assigned to different conditions (with this assignment counterbalanced across participants). The sentences were assigned to (1) *Pure Reading* (i.e., reading without conflict from memory recall); (2) *Conflict Reading* (i.e., reading with conflict from memory recall) and (3) *Conflict Recall* (i.e., memory recall with conflict from semantic input). Similarly, the autobiographical memory cues were assigned to (1) *Pure Recall* (i.e., memory recall without conflict from semantic input); (2) *Conflict Recall* (i.e., memory recall with conflict from semantic input) and (3) *Conflict Reading* (i.e., reading with conflict from memory recall). The words used in these conditions were matched on key psycholinguistic variables (see Table 1): they did not differ in lexical frequency (CELEX database; Baayen et al. 1993) (Reading: $F(2,46) = .80$, $p = .46$, $\eta_p^2 = .03$; Recall: $F(2,46) = .19$, $p = .83$, $\eta_p^2 = .01$), imageability (Davis 2005)

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(Reading: $F(2,46) = .20$, $p = .82$, $\eta_p^2 = .01$; Recall: $F(2,46) = 1.07$, $p = .35$, $\eta_p^2 = .04$) or concreteness (Brysbaert et al. 2014) (Reading: $F(2,46) = .21$, $p = .81$, $\eta_p^2 = .01$; Recall: $F(2,46) = .13$, $p = .88$, $\eta_p^2 = .01$). In addition, all the words in the three sets of sentences were comparable across these variables (see **Table 1**; Frequency: $F(2,46) = 1.40$, $p = .26$, $\eta_p^2 = .06$; Imageability: $F(2,46) = .30$, $p = .74$, $\eta_p^2 = .01$; Concreteness: $F(2,46) = .70$, $p = .50$, $\eta_p^2 = .03$). Two additional cue words were created for task practice. There was no overlap in the words presented as autobiographical cues or key words within sentences.

Table 1. *Linguistic properties of each set of key words within sentences and autobiographical memory cues, and the words within each set of sentences (M ± SD). Sets (i), (ii), and (iii), were counterbalanced across participants (see Materials).*

Conditions	***Frequency***	***Imageability***	***Concreteness***
(i) sentence key words	1.31 ± .56	591.67 ± 34.20	4.74 ± .52
(ii) sentence key words	1.47 ± .50	598.05 ± 27.49	4.72 ± .55
(iii) sentence key words	1.29 ± .52	592.61 ± 44.35	4.64 ± .58
(i) autobiographical memory cues	1.59 ± .76	588.48 ± 41.20	4.70 ± .47
(ii) autobiographical memory cues	1.48 ± .62	594.64 ± 24.46	4.75 ± .30
(iii) autobiographical memory cues	1.54 ± .56	601.53 ± 23.65	4.73 ± .41
(i) sentence materials	2.59 ± .24	354.34 ± 27.41	2.72 ± .26
(ii) sentence materials	2.52 ± .20	352.40 ± 23.39	2.72 ± .21
(iii) sentence materials	2.48 ± .27	347.64 ± 35.24	2.80 ± .24

2.4. Procedure

Testing occurred across two consecutive days with autobiographical memory generation on Day 1 and memory recall and reading in the scanner on Day 2.

Autobiographical memory generation task on Day 1. Participants were asked to generate their own personal memories from cue words (i.e., Party) outside the scanner. These memories could be from

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any time, from childhood to the day before testing. Participants were asked to identify specific events that they were personally involved in and to provide as much detail about these events as they could. These details included when and where the event took place, who was involved, what happened, and the duration. To ensure compliance with the task instructions, participants typed these details into a spreadsheet, which ensured that comparable information was recorded for the different cue words.

Autobiographical memory recall and reading task on Day 2. On the following day, participants were asked to read sentences for comprehension or recall their generated personal memories inside the scanner. In reading trials, sentences were presented word by word, after either (1) an autobiographical memory cue word (e.g., Party) associated with a personal memory outside the scanner, creating conflict between task-relevant and task-irrelevant patterns of semantic retrieval, or (2) a letter string (XXX) allowing reading to take place in the absence of conflict from autobiographical memory. We controlled the duration of the sentences by presenting the words on 15 successive slides, combining short words on a single slide (e.g., *have been* or *far better*) and presenting articles and conjunctions together with nouns (e.g., *the need*; *and toys*). In memory recall trials, participants were asked to recall autobiographical memories during the presentation of either (1) an unrelated sentence, creating conflict between task-relevant and task-irrelevant patterns of semantic retrieval or (2) letter strings (XXX) allowing autobiographical memory to take place without distracting semantic input. In this way, we manipulated potential conflict between autobiographical memory and reading comprehension. As a control condition, meaningless letter strings (i.e., xxxxx) were presented. Participants were asked to view these strings and perform a low-level baseline task (colour-change detection, common across all conditions; see below).

As shown in Figure 1, each trial started with a fixation cross presented for a jittered interval of 1-3s in the centre of the screen. Then either an autobiographical memory cue word or a letter string (e.g., “XXX”) appeared for 2s. Cue words and single letter strings preceded the presentation of sentences and repeated letter strings, which were presented inside a black rectangle. During the presentation of the cue word, participants were asked to bring to mind their personal memory related to this item. Next, the task instruction (i.e. READING or MEMORY RECALL) was presented for 1s to instruct the participants to focus on either reading comprehension or memory recall. For the letter string baseline, a capitalised meaningless letter string (e.g., “XXXXX”) was presented during task instruction period. Following that,

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sentences or letter strings were presented item-by-item, with each one lasting 600ms. On memory recall trials, participants were asked to keep thinking about their autobiographical memory, in as much detail as possible, until the end of the trial. In order to ensure the participants were maintaining attention to the presented stimuli (even when these were irrelevant and creating competition), they were told to press a button when they noticed the colour of a word or letter string change to red. There were 3 trials out of 24 trials in each condition that involved responding in this way.

After each trial, participants were asked to rate several dimensions of their experience. For the reading comprehension task, participants were asked about task focus (i.e., How well did you focus on the reading task?), as well as about their comprehension (i.e., How well did you comprehend this sentence?), and conceptual familiarity (i.e., How familiar were you with the reading content?). For autobiographical memory trials, participants were asked the same question about task focus (i.e., How well did you focus on the recall task?), vividness (i.e., How vivid was your memory?), and consistency of their memory recall (i.e., How similar was it to your previously generated memory?).

The three rating questions were sequentially presented after a jittered fixation interval lasting 1-3s. Participants were required to rate these characteristics on a scale of 1 (not at all) to 7 (very well) by pressing a button box with their right hand. They had 4s to make each response. There were no ratings for the letter string trials.

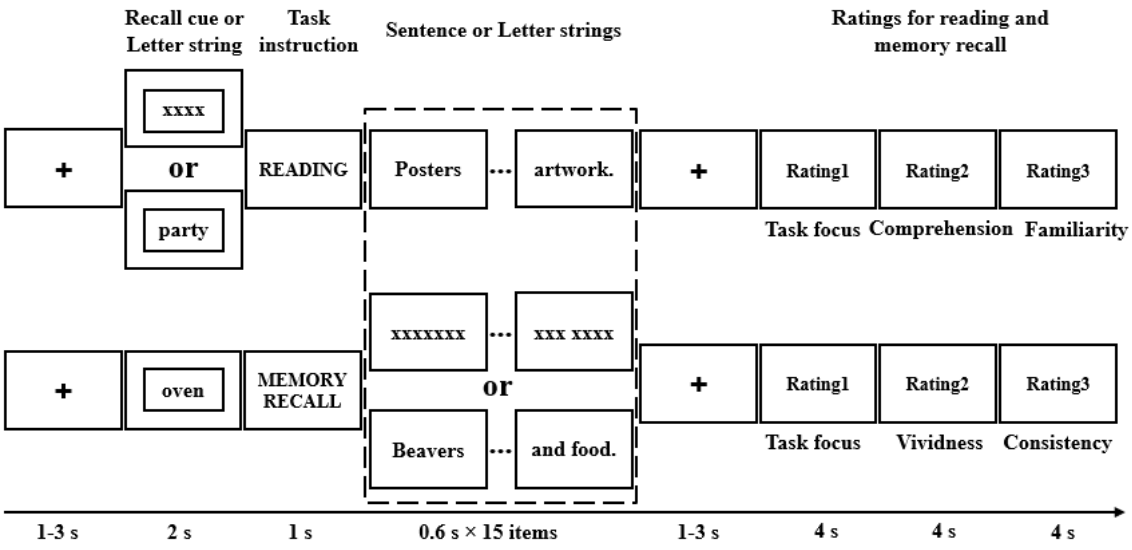

***Figure 1*. Task illustration.** Procedure of reading task and autobiographical memory recall in the scanner on Day 2.

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We examined text-based memory for the reading sentences presented in the *Pure reading*, *Conflict reading*, and *Conflict recall* conditions immediately after the scanning session. Participants were presented with the cue words from the reading lists, one at a time, and were asked to try to recall any words from the sentences that they had seen inside the scanner relating to this cue word. They typed their responses. Participants were told in advance that they would be asked about the sentences that they had read in the scanner.

Stimuli were presented in four runs, with each containing 30 trials: 6 trials in each of the four experimental conditions, and 6 letter string trials. Each run lasted 12.85 minutes, and trials were presented in a pseudorandom order to make sure that the trials from the same experimental condition were not consecutively presented more than three times. The runs were separated by a short break and started with a 9-second alerting slide (i.e. Experiment starts soon).

Before entering the scanner, participants completed a 6-minute task to test their memory of the generated personal memories that they came up with on the day before scanning. In this task, each autobiographical cue was presented for 3s after a jittered interval of 1-3s in the centre of the screen, with two options (i.e., *Remembered* and *Not remembered*). Participants pressed one of two buttons on a keyboard to indicate if they could remember the memory they previously came up with and they then reviewed their generated memories to refresh themselves with the ones that were not well remembered (these reviews were needed in a mean of 29.2% of trials; SD = 12.4%). Next, detailed instructions were provided for the in-scanner memory recall and reading tasks. To ensure participants fully understood the task requirements, they completed an 8-trial practice block containing all types of conditions. They were given feedback about their performance and, if necessary, they repeated the practice trials (this additional training was only needed for one participant to practice providing rating responses within 4s).

2.5. Neuroimaging data acquisition

Structural and functional data were acquired using a 3T GE HDx Excite Magnetic Resonance Imaging (MRI) scanner utilizing an eight-channel phased array head coil at the York Neuroimaging Centre, University of York. Structural MRI acquisition in all participants was based on a T1-weighted 3D fast spoiled gradient echo sequence (repetition time (TR) = 7.8 s, echo time (TE) = minimum full, flip angle = 20°, matrix size = 256 × 256, 176 slices, voxel size = 1.13 mm × 1.13 mm × 1 mm). The task-

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based activity was recorded using single-shot 2D gradient-echo-planar imaging sequence with TR = 3 s, TE = minimum full, flip angle = 90°, matrix size = 64 × 64, 60 slices, and voxel size = 3 mm × 3 mm × 3 mm. Data was acquired in a single session. The task was presented across 4 functional runs, with each containing 257 volumes.

2.6. Pre-processing of task-based fMRI data

All functional and structural data were pre-processed using a standard pipeline and analysed via the FMRIB Software Library (FSL version 6.0, www.fmrib.ox.ac.uk/fsl). Individual T1-weighted structural brain images were extracted using FSL's Brain Extraction Tool (BET). Structural images were linearly registered to the MNI152 template using FMRIB's Linear Image Registration Tool (FLIRT). The first three volumes (i.e. the presentation of the 9-second-task-reminder 'Experiment starts soon') of each functional scan were removed in order to minimise the effects of magnetic saturation, therefore there was a total of 254 volumes for each functional scan. The functional neuroimaging data were analysed using FSL's FMRI Expert Analysis Tool (FEAT). We applied motion correction using MCFLIRT (Jenkinson et al. 2002), slice-timing correction using Fourier space time-series phase-shifting (interleaved), spatial smoothing using a Gaussian kernel of FWHM 6 mm, and high-pass temporal filtering (sigma = 100 s) to remove temporal signal drift. In addition, motion scrubbing (using the fsl_motion_outliers tool) was applied to exclude volumes that exceeded a framewise displacement threshold of 0.9. There were no scans with greater than 25% of the data censored for motion, and thus no participants or scans were excluded from the univariate analysis due to excessive motion.

2.7. Univariate analysis of task-based fMRI data

The analysis examined the common and differentiated brain regions that are important for reading comprehension and autobiographical memory retrieval. We also identified the response to conflict when participants either read the sentences with or without an autobiographical memory cue, or recalled their generated memories with or without conflict from sentence presentation. Consequently, the model included two factors within a 2x2 design: (1) Task (Reading Comprehension vs. Autobiographical Memory Recall), and (2) Conflict (No Conflict vs. Conflict). In addition, we included task focus ratings on each trial as a parametric regressor to identify brain responses that related to how well participants had been able to engage with the reading and memory recall tasks.

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The pre-processed time-series data were modelled using a general linear model, using FMRIB's Improved Linear Model (FILM) correcting for local autocorrelation (Woolrich et al. 2001). Nine Explanatory Variables (EV) of interest and nine of no interest were modelled using a double-Gaussian hemodynamic response gamma function. The nine EVs of interest were: (1) *Pure Reading* (i.e., no conflict from memory recall) and (2) *Conflict Reading* (i.e., conflict from memory recall), (3) *Pure Recall* (i.e., no conflict from semantic (reading) input) and (4) *Conflict Recall* (i.e., conflict from semantic (reading) input), (5) Letter String Baseline, (6-9) Task Focus effect during the target for each of the four experimental conditions as a parametric regressor. Our EVs of no interest were: (10) Cue words related to the generated memories and (11) Letter strings before the presentation of task instructions, Task instructions for (12) *Pure Reading*, (13) *Conflict Reading* (this separation of the task instruction period on reading trials was based on the consideration that some recall or task preparation was likely to be occurring in the *Conflict recall* condition due to the presentation of autobiographical memory cues), plus task instructions for (14) *Memory Recall* and (15) *Letter String* baseline conditions. Other EVs of no interest were: (16) Fixation (the inter-stimulus fixations between the sentences or letter strings and the ratings questions, when some semantic retrieval may have been ongoing), (17) Responses to catch trials (which included all time points with responses across conditions), and (18) Rating decision periods (including all the rating questions across experimental conditions). EVs for each condition commenced at the onset of the first word of the sentence or the first letter string (when meaningless items were presented over the same period), with EV duration set as the presentation time (9s). The parametric EVs for the effect of Task Focus during the target had the same onset time and duration as the EVs corresponding to the four experimental trials, but in addition included the demeaned Task Focus ratings value as a weight. The fixation period between the trials provided the implicit baseline.

In addition to contrasts examining the main effects of Task (Reading Comprehension vs. Autobiographical Memory Recall), and Conflict (No Conflict vs. Conflict), we included all two-way interaction terms for both the main experimental conditions and the effect of Task Focus (which was included as a parametric regressor for each experimental condition), and comparisons of each experimental condition with the letter string baseline, which allowed us to identify the activation and deactivation in each task as well as common activation across tasks by performing formal conjunction analysis. The four

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sequential runs were combined using fixed-effects analyses for each participant. In the higher-level analysis at the group level, the combined contrasts were analysed using FMRIB's Local Analysis of Mixed Effects (FLAME1), with automatic outlier de-weighting (Woolrich 2008). A 50% probabilistic grey-matter mask was applied. Clusters were thresholded using Gaussian random-field theory, with a cluster-forming threshold of $z = 3.1$ and a familywise-error-corrected significance level of $p = .05$.

2.8. Psychophysiological interaction analysis

In the formal conjunction analysis of the contrast maps of each experimental condition against the letter string baseline, we identified that inferior frontal gyrus and lateral temporal cortex regions within the lateral temporal DMN subsystem were involved in both tasks (see Figure 5). Also, the core DMN regions were more important for autobiographical memory recall identified by the contrast of tasks (see Figure 6B). In order to establish how these DMN subsystems support both reading and memory recall, we conducted psychophysiological interaction (PPI) analysis.

The lateral temporal DMN conjunction and core DMN regions from the *Autobiographical memory > Reading* contrast map were used as the seeds and their time series were extracted. We then ran two separate models to examine connectivity of each DMN subsystem seed, which included all the regressors in the basic task model described above (18 regressors and motion regressor), a PPI term for each of the four experimental conditions (*Pure Reading*, *Conflict Reading*, *Pure Recall*, and *Conflict Recall*), a PPI term for the Task Focus ratings for each experimental condition (to reveal which regions showed increased connectivity as task focus increased), as well as the time series of DMN subnetwork seeds, using the generalized psychophysiological interaction (gPPI) approach (McLaren et al. 2012). The regressors were not orthogonalized. This analysis applied the same contrasts and cluster forming threshold as the univariate model. We also applied Bonferroni correction to account for the fact that we included two models (seeding from common activation within the lateral temporal DMN subsystem and core DMN sites), the *p*-value consequently accepted as significant was $p < 0.025$. For the analysis to test relationship between functional connectivity and behavioural performance (i.e., ratings inside the scanner and sentence recall outside the scanner), all variables were *z*-transformed and outliers more than 2.5 standard deviations above or below the mean were identified and imputed with the cut-off value (i.e., +/- 2.5) prior to data analysis.

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3. Results

3.1. Results outline

First, we describe the behavioural results. Second, we report univariate analyses in which we first identify brain regions showing activation and deactivation during reading and autobiographical memory recall, relative to a letter string baseline. To better understand the key similarities and differences in brain activity between internally- and externally-oriented tasks, we consider the location of this activation/deactivation along the principal gradient capturing the separation between heteromodal DMN and unimodal cortex (Margulies *et al.* 2016), and consider the relevance of these findings for DMN subsystems. Third, we describe (i) commonalities (identified by using a formal conjunction analysis) and differences (identified by task contrasts) across autobiographical memory and reading tasks; and (ii) effects of task conflict and task focus – i.e., regions in which activation correlated with rated focus on each trial. To anticipate our key findings, we found that both reading and autobiographical memory elicited activation at both the top and bottom ends of the principal gradient of cortical organisation, in sensorimotor areas such as visual cortex and heteromodal semantic regions. These patterns of activation did not differ along the principal gradient: the heteromodal response in reading and autobiographical memory was equally close to the apex. However, the tasks elicited strikingly different patterns of deactivation. These task similarities and differences were related to previously-described DMN subsystems: both tasks elicited activation within a subnetwork of DMN focussed on left lateral temporal cortex, while core DMN regions (e.g. posterior cingulate cortex and medial prefrontal cortex) showed activation during memory recall and deactivation during reading. The parametric effect of task focus revealed that both activation and deactivation within core DMN can be beneficial to cognition. Finally, PPI analysis established how common DMN regions within the lateral temporal subsystem show different patterns of connectivity during reading comprehension and memory recall.

3.2. Behavioural results

Results of catch trials: Participants detected 75.6% of colour-change catch trials (i.e., they responded to this percentage of catch trials across conditions), showing that they were paying attention to inputs presented on the screen. Repeated-measures ANOVAs examining accuracy, RT, and response efficiency (i.e., RT divided by accuracy), and assessing the effects of Task (Reading vs. Autobiographical

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memory recall) and Conflict (No conflict vs. Conflict), revealed there were no differences in colour-change detection rates across conditions (see Figure 2A); trials with no response were excluded from the RT analysis (24.4%). There was no main effect of Task (Accuracy: $F(1,28) = 1.54$, $p = .22$, $\eta_p^2 = .05$; RT: $F(1,28) = 1.92$, $p = .18$, $\eta_p^2 = .06$; Response efficiency: $F(1,28) = .35$, $p = .56$, $\eta_p^2 = .01$), no main effect of Conflict (Accuracy: $F(1,28) = .27$, $p = .61$, $\eta_p^2 = .01$; RT: $F(1,28) = 2.83$, $p = .10$, $\eta_p^2 = .001$; Response efficiency: $F(1,28) = 1.22$, $p = .28$, $\eta_p^2 = .04$), and no interaction (Accuracy: $F(1,28) = .85$, $p = .36$, $\eta_p^2 = .03$; RT: $F(1,28) = 1.27$, $p = .27$, $\eta_p^2 = .04$; Response efficiency: $F(1,28) = .95$, $p = .34$, $\eta_p^2 = .03$).

We also performed paired-samples *t*-tests (Bonferroni-corrected for four comparisons) comparing colour-change detection for each experimental condition with the letter string baseline (RT: $M \pm SD = .53 \pm .17$ s; Accuracy: $M \pm SD = 74.7 \pm 24.5$ %; Response efficiency: $M \pm SD = .85 \pm .57$). Responses to baseline trials were significantly faster than for reading or recall trials ($t(28) > 2.84$, $p < .009$). For both accuracy and response efficiency, there were no significant differences between the experimental tasks and the letter string baseline data ($t(28) < 1$).

Results of ratings on each task trial: Figure 2B summarises the ratings participants provided after each reading and autobiographical memory recall trial. For Task Focus ratings, a 2 (Reading vs. Autobiographical recall) by 2 (No conflict vs. Conflict) repeated-measures ANOVA revealed main effects of both Task ($F(1,28) = 4.76$, $p = .038$, $\eta_p^2 = .15$) and Conflict ($F(1,28) = 44.28$, $p < .001$, $\eta_p^2 = .61$): people rated their task focus as higher for the reading task, and they were more focussed on both tasks when there was no conflict. There was no interaction between these factors, $F(1,28) = .12$, $p = .73$, $\eta_p^2 = .004$, suggesting that the effect of conflict was similar across both tasks.

Paired-samples *t*-tests were used to examine the effect of task conflict on other ratings (which were different across the two tasks). People rated their sentence comprehension as higher when there was no task conflict ($t(28) = 3.22$, $p = .003$). There was no difference in participants' rated familiarity with the information in the sentences across conditions ($t(28) = 1.45$, $p = .16$). The participants also rated their autobiographical memories as more vivid ($t(28) = 6.02$, $p < .001$) and more consistent with their previously generated memories ($t(28) = 2.86$, $p = .008$) when there was no task conflict.

Pearson's correlation analysis revealed that these different ratings were highly correlated. For reading, task focus correlated with comprehension ($r = .71$, $p < .001$), comprehension correlated with

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familiarity (r = .41, p < .001) and task focus correlated with familiarity (r = .29, p < .001). For autobiographical memory, task focus correlated with vividness (r = .68, p < .001), vividness correlated with consistency (r = .54, p < .001) and task focus correlated with consistency (r = .47, p < .001). For this reason, only the parametric effect of task focus was included in the fMRI analysis.

Results of post sentence recall: We also calculated the percentage of words recalled correctly for each sentence across *Pure Reading*, *Conflict Reading*, and *Conflict Recall* conditions, since memory for the text was expected to relate to task focus. The *Pure Reading* condition had better recall ($M \pm SD$ = 15 ± 9 %) than the *Conflict Reading* condition ($M \pm SD$ = 12 ± 8 %; $t(28)$ = 2.93, p = .007), while the poorest memory for the text occurred in the *Conflict Recall* condition ($M \pm SD$ = 2 ± 3 %), when participants were actively trying to ignore the sentence ($t(28)$ = 6.08, p < .001). The percentage of words recalled in the reading task was positively correlated with task focus (*Pure Reading*: r = .30, p < .001; *Conflict Reading*: r = .29, p < .001) and comprehension (*Pure Reading*: r = .10, p = .009; *Conflict Reading*: r = .37, p < .001). These results taken together show that conflict from the autobiographical memory cues impaired sentence recall outside the scanner.

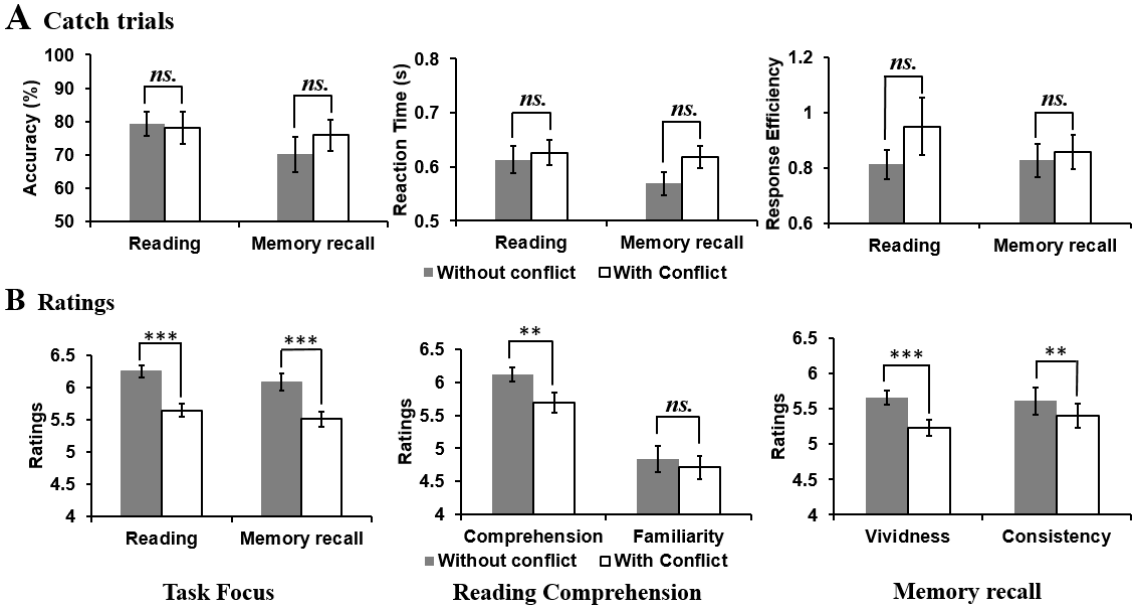

Figure 2. **Behavioural results. A)** Accuracy (percentage correct, left panel) and reaction time (in seconds, middle panel), as well as response efficiency (right panel) for the catch trials in each experimental condition (*Pure Reading*, *Conflict Reading*, *Pure Recall*, and *Conflict Recall*). **B)** Ratings for task focus (left panel) in each experimental condition, comprehension and familiarity with sentence content in both reading conditions

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(middle panel), and vividness and consistency with previously generated memory in both memory recall conditions (right panel). Error bars represent the standard error. *** indicates $p < .001$; ** indicates $p < .01$; *ns.* indicates *not significant.*

3.3. fMRI results

3.3.1. Activation and deactivation in reading and autobiographical memory

To identify activation and deactivation elicited by each task, we performed a formal conjunction analysis on the contrast maps of conflict and no-conflict for each experimental condition over the letter string baseline (providing a basic level of control for visual input and button presses; maps for each experimental condition over letter string baseline are shown in Figure S1 in the supplementary materials). For reading, the bilateral temporal regions (i.e., temporal poles, superior/middle/inferior temporal gyrus), precentral gyrus, middle/inferior frontal gyrus, temporal fusiform cortex, supplementary motor cortex, and visual cortex showed activation relative to the letter string baseline (see Figure 3A; the conjunction of *Pure reading* > *Baseline* and *Conflict reading* > *Baseline*), while bilateral middle frontal gyrus, supramarginal gyrus, medial prefrontal gyrus, anterior/posterior cingulate gyrus, and precuneus showed deactivation (see Figure 3B; the conjunction of *Baseline* > *Pure reading* and *Baseline* > *Conflict reading*). For autobiographical memory, middle temporal gyrus, temporal pole, middle/inferior frontal gyrus, insular cortex, supplementary motor cortex, and visual cortex showed activation compared to the letter string baseline (see Figure 3C; the conjunction of *Pure recall* > *Baseline* and *Conflict recall* > *Baseline*), while supramarginal gyrus showed deactivation (see Figure 3D; the conjunction of *Baseline* > *Pure recall* and *Baseline* > *Conflict recall*).

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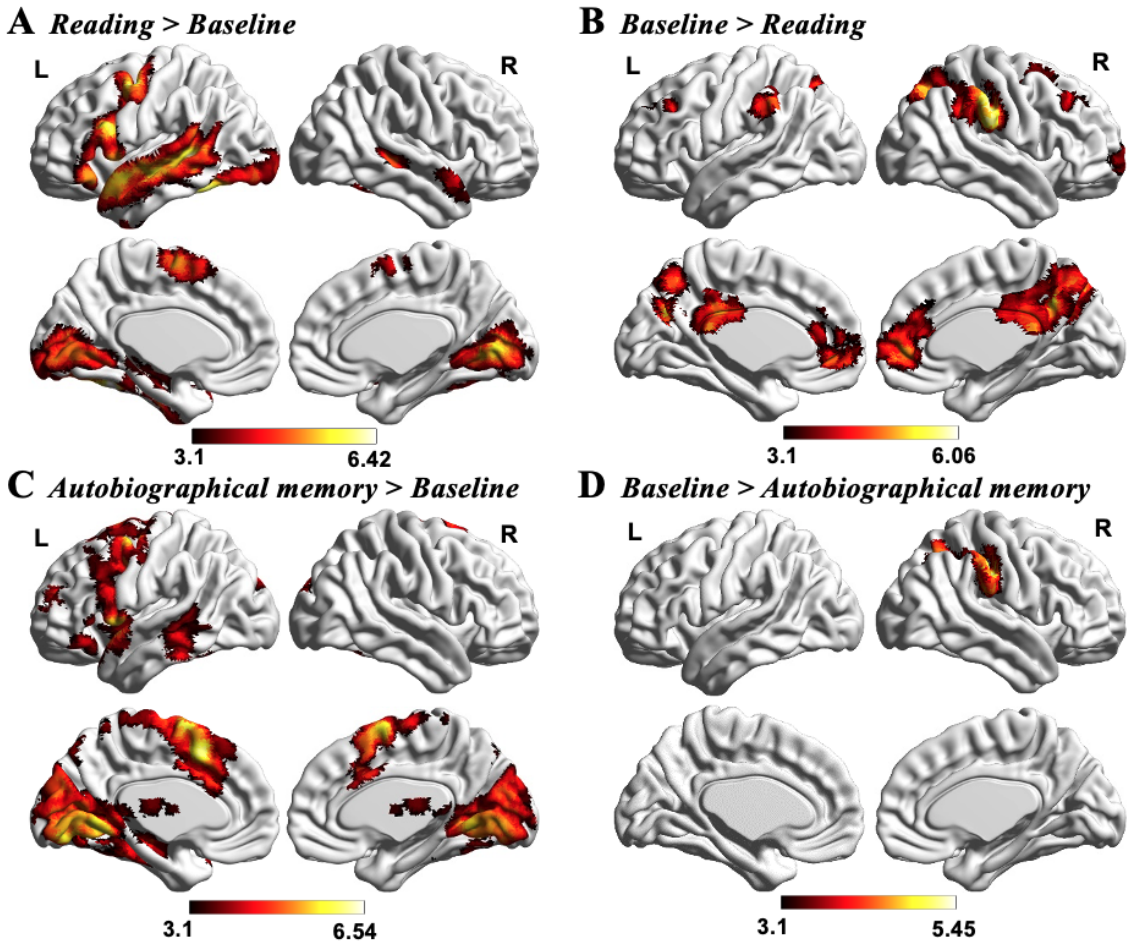

Figure 3*. Task activation and deactivation. A) *Reading* > *Baseline and **B) *Baseline* > *Reading*** show the brain activation and deactivation during reading task relative to the letter string baseline. **C) *Autobiographical memory* > *Baseline*** and **D) *Baseline* > *Autobiographical memory*** show the brain activation and deactivation during autobiographical memory recall relative to the letter string baseline. These conjunctions were identified using FSL's 'easythresh_conj' tool. All maps were thresholded at $z > 3.1$ ($p < .05$). L = Left hemisphere; R = Right hemisphere.

Next, we extracted the principal gradient values of each voxel within the maps in Figure 3, to characterise the distribution of activation and deactivation in each task, relative to the low-level baseline, along the principal gradient. The principal gradient captures the separation between unimodal systems (in blue in Figure 4A) and heteromodal regions within DMN (in red in Figure 4A; Margulies *et al.* 2016). We found that both reading and autobiographical memory elicited activation in unimodal and heteromodal cortex, while reading elicited greater deactivation within the DMN (see Figure 4B). We employed a bin-

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by-bin analysis to compare the activation and deactivation elicited by the tasks along the principal gradient. The whole-brain principal gradient map was evenly divided into 10 bins based on the rank of gradient values from the lowest to the highest values (see Figure 4C). The number of voxels within each bin that showed activation and deactivation was then counted for each participant, thresholded in our main analysis at $z > 2.6$ (bins with 0 activating and deactivating voxels at this threshold were 1.6% and 6.0% of the total, respectively. The same patterns were observed when replacing these 0s with mean). A 2 (Activity: *Activation* vs. *Deactivation*) by 2 (Task: *Reading* vs. *Autobiographical memory*) by 10 (Gradient bins) repeated-measures ANOVA found a three-way interaction, $F(9,252) = 6.70$, $p < .001$, $\eta_p^2 = .19$. Separate ANOVAs revealed that the interaction between Task and Bin was significant for both states of activity, with a greater interaction for deactivation, $F(9,252) = 10.75$, $p < .001$, $\eta_p^2 = .28$, compared to activation, $F(9,252) = 2.96$, $p = .002$, $\eta_p^2 = .10$. Tests of simple effects revealed that the pattern of activation was similar between reading and autobiographical memory recall across the whole principal gradient (p values > .09 across all the bins: see Figure 4C). However, reading elicited greater deactivation than autobiographical memory, especially towards the DMN end of the gradient (in bins 5 - 10 and 2; p values < .004; see Figure 4C; see Supplementary Table S1 for detailed results). Similar patterns of task activation and deactivation were found when the individual maps were thresholded at a lower threshold of $z > 2.3$ (bins with 0 activating and deactivating voxels at this threshold were 0.6% and 2.8% of the total, respectively; see Supplementary Figure S2). In summary, both tasks elicited activation within heteromodal DMN at the top of the gradient, and within sensorimotor areas at the bottom of the gradient, but reading also evoked greater deactivation in other DMN regions. Below, we relate this pattern of similar DMN activation yet differential DMN deactivation across tasks to the distinction between DMN subsystems.

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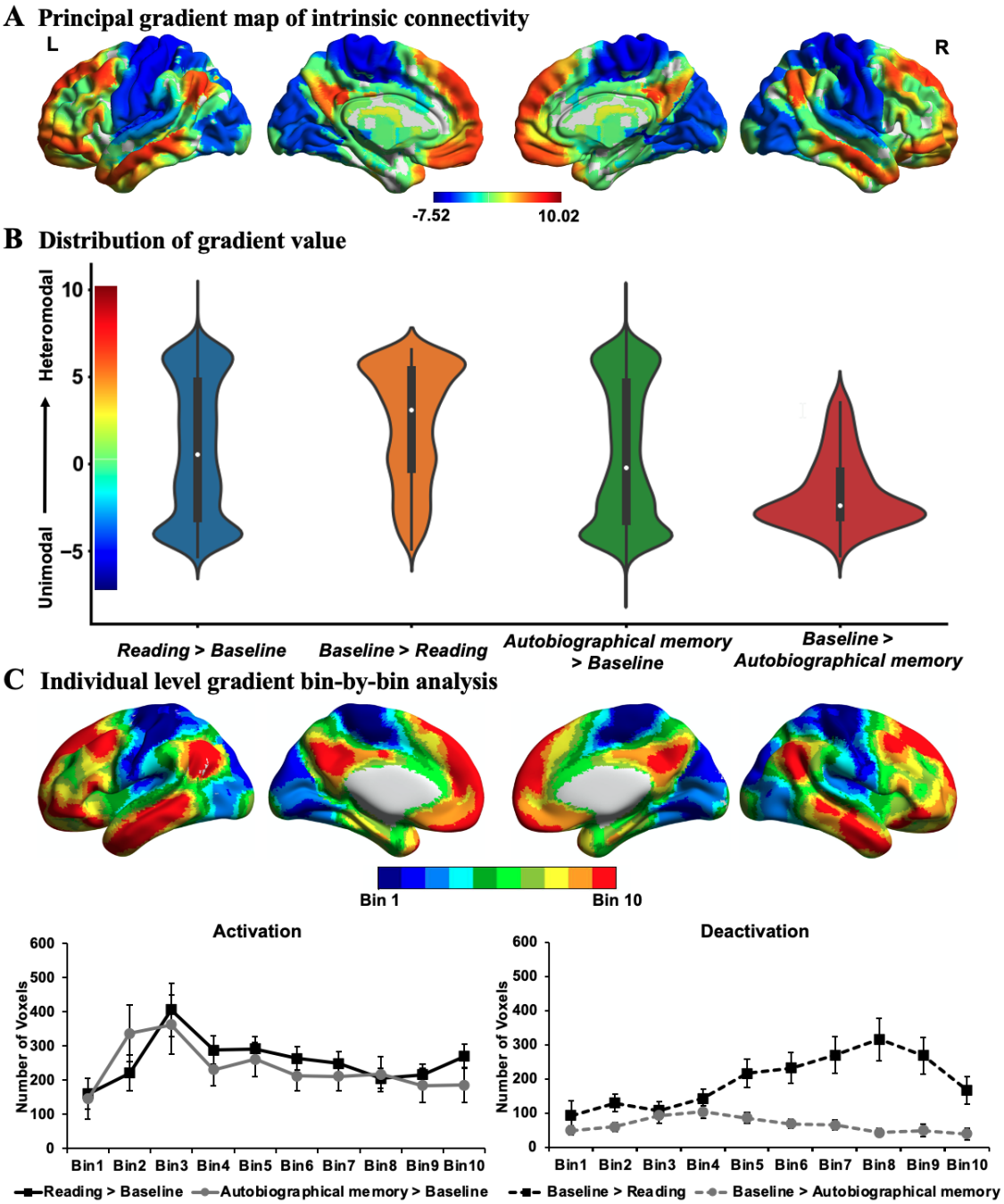

***Figure* 4. A)** Principal gradient map of intrinsic connectivity from Margulies *et al.* (2016) capturing the transition between unimodal regions (cold colours) and heteromodal regions corresponding to the DMN (warm colours). **B)** The violin plots show the distribution of gradient values extracted from each conjunction map. **C)** The whole-brain map was evenly divided into 10 bins from the bottom to the top of the principal gradient. The line charts present the activation and deactivation in each task each bin relative to the letter string baseline. Error bars represent the standard error.

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3.3.2. Common activation in both reading and autobiographical memory recall tasks

Next, we examined the brain regions activated in both reading comprehension and autobiographical memory recall tasks in a whole-brain analysis. We computed a formal conjunction across the contrast maps of each task over the letter string baseline and established that they overlapped in precentral gyrus, middle/inferior frontal gyrus, temporal pole, middle temporal gyrus, temporal fusiform cortex, supplementary motor cortex, parahippocampus and visual cortex (intracalcarine cortex and lingual gyrus; see Figure 5A). The mean percentage signal change of each experimental condition over baseline in each cluster is presented in Figure 5A. The lateral temporal clusters and inferior frontal gyrus largely fell within the DMN, as defined by Yeo *et al.* (2011) in a 7-network parcellation of whole-brain intrinsic connectivity in 1000 brains (DMN shown in blue in Figure 5B with overlap in pink). We also compared these regions of overlap with three DMN subsystems – core DMN, lateral temporal subsystem and medial temporal subsystem – defined by Yeo *et al.* (2011) in their 17-network parcellation of intrinsic connectivity patterns. Of those voxels which fell within DMN, 95% were within the DMN subnetwork that encompasses lateral temporal cortex, anterior and ventral portions of IFG and dorsomedial prefrontal cortex (see Figure 5C with pie chart showing the percentage of overlap with each subsystem). We refer to this network as the "lateral temporal DMN subsystem" below. In summary, this analysis shows that lateral temporal DMN regions are implicated in *both* reading comprehension and autobiographical memory.

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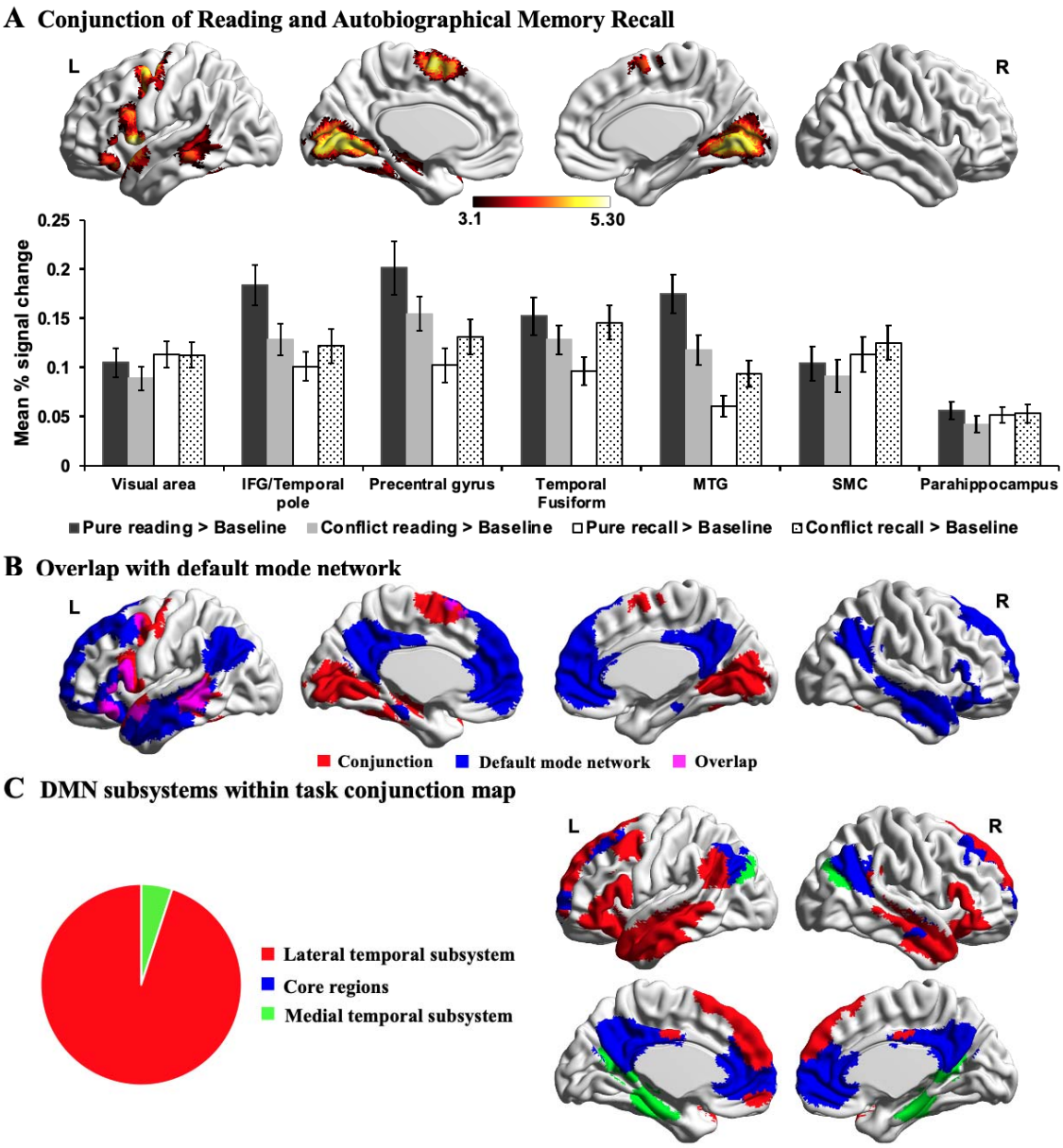

***Figure 5*. Conjunction analysis. A)** Conjunction of brain activation during reading comprehension and autobiographical memory recall, with this conjunction identified using FSL's 'easythresh_conj' tool. The bar chart shows the mean % signal change of each experimental condition over baseline in each identified cluster. Error bars represent the standard error. **B)** These conjunction clusters overlapped with the default mode network (DMN; in blue) defined by Yeo *et al*. (2011) in a 7-network parcellation of whole-brain intrinsic connectivity for 1000 brains (overlap in pink). **C)** The pie chart illustrates the percentages of voxels that were within the DMN in the task conjunction map that overlap with each DMN subsystem. Subsystems were defined by Yeo *et al*. (2011) in a 17-network parcellation of whole-brain functional connectivity for 1000 brains: the medial

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temporal subsystem is shown in green, core DMN is shown in blue and the lateral temporal subsystem is shown in red. The DMN conjunction largely fell within the lateral temporal subsystem of DMN. All maps were thresholded at $z > 3.1$ ($p < .05$). IFG = inferior frontal gyrus; MTG = middle temporal gyrus; SMC = supplementary motor cortex; L = Left hemisphere; R = Right hemisphere. The maps are fully saturated to emphasize the regions of overlap.

3.3.3. Main effects in task-based fMRI

Effects of Task: Next, we examined differences in activation across tasks. The contrast of *Reading* > *Autobiographical memory* elicited activation in left inferior frontal gyrus, lateral temporal cortex (including temporal poles, superior/middle/inferior temporal gyrus), and visual cortex (including occipital pole, occipital fusiform gyrus, and lateral occipital cortex; see Figure 6A). In contrast, *Autobiographical memory* > *Reading* activated bilateral superior/middle frontal gyrus, frontal pole, insular cortex, medial prefrontal gyrus, anterior/posterior cingulate gyrus, precuneus, angular gyrus, and lingual gyrus (see Figure 6B). In order to further understand task differences across the sub-networks within DMN, we overlapped these reading and recall maps with the core, lateral temporal, and medial temporal subsystems defined by Yeo *et al*.'s (2011) 17-network parcellation. DMN regions highlighted by the *Reading* > *Autobiographical memory* contrast almost fully fell within the lateral temporal subsystem (see Figure 6C), while the *Autobiographical memory* > *Reading* contrast showed greater overlap with core DMN regions (see Figure 6D).

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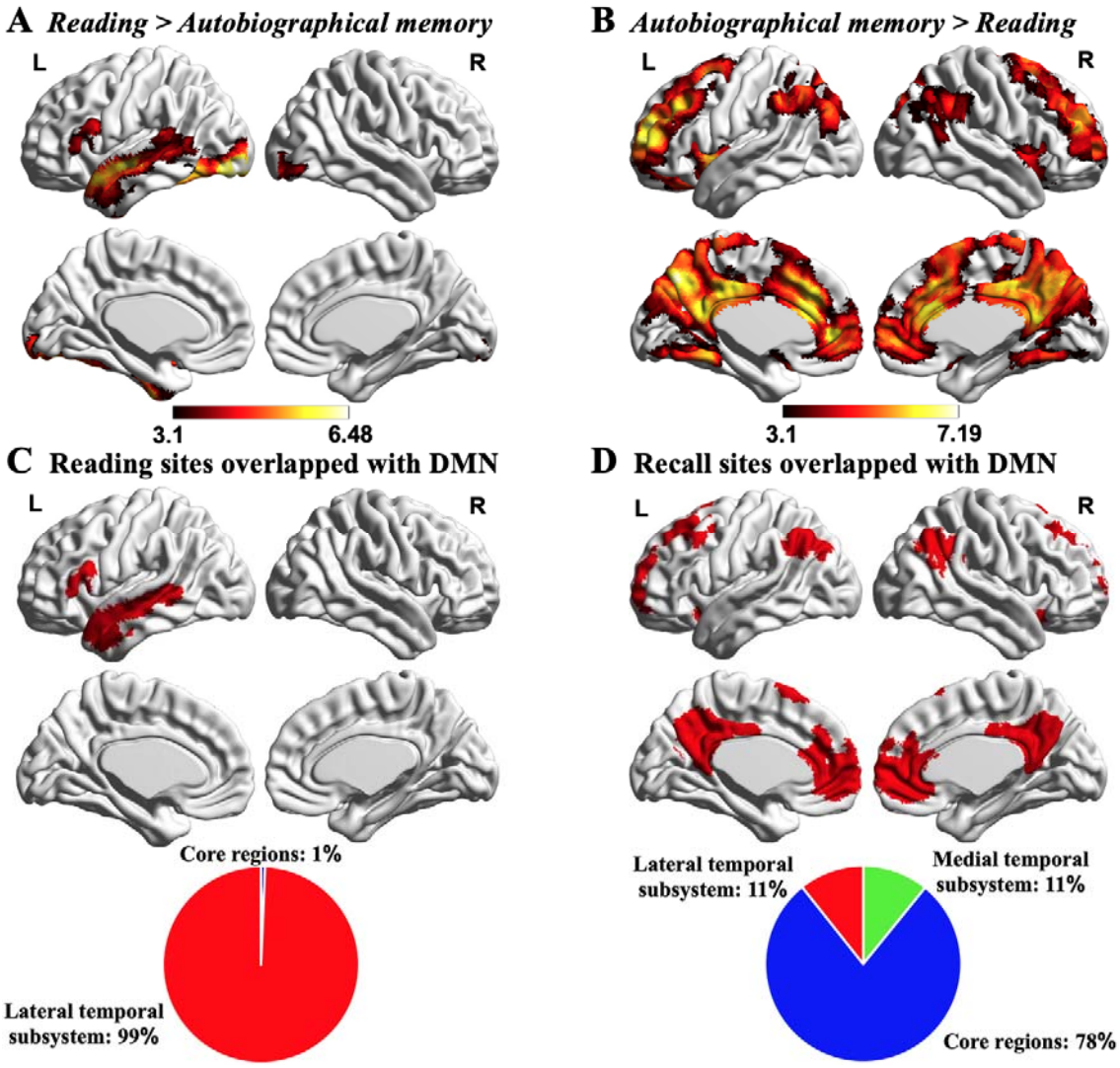

***Figure 6*. Effects of Task. A)** Significant activation in reading defined using the contrast of *Reading* > *Autobiographical memory*. **B)** Significant activation in autobiographical memory defined using the contrast of *Autobiographical memory* > *Reading*. **C-D)** The overlap of *Reading* > *Autobiographical memory* and *Autobiographical memory* > *Reading* contrast maps with DMN. The pie charts at the bottom illustrate the percentage of overlap of reading and recall maps with each DMN subsystem, respectively. All maps were thresholded at $z > 3.1$ ($p < .05$). L = Left hemisphere; R = Right hemisphere.

Having established that reading and autobiographical memory recruit distinct DMN sub-systems, we asked where these tasks fall on the principal gradient of connectivity. One possibility is that the core sub-network, which was activated more strongly by autobiographical memory retrieval, is further up the

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gradient than reading, since in the latter task, visual input drives conceptual retrieval. Alternatively, the apex of different DMN subsystems might occupy the same position on the principal gradient. To investigate whether reading and autobiographical memory reached the same gradient apex value, we extracted the maximum gradient value for each individual participant within the task contrast maps thresholded at $z > 3.1$, masked by DMN. Four participants were excluded from this analysis because there was no relevant activation. A paired samples *t*-test showed no significant task difference in maximum DMN gradient values across people (Reading: $M \pm SD = 6.38 \pm 1.13$; Autobiographical memory: $M \pm SD = 6.51 \pm .69$; $t(24) = -.53$, $p = .60$; the same pattern was found when the threshold was set at 2.6: Reading: $M \pm SD = 6.66 \pm .18$; Autobiographical memory: $M \pm SD = 6.68 \pm .20$; $t(26) = -.36$, $p = .72$). We also examined the DMN subnetworks themselves, and found gradient values within the lateral temporal DMN subsystem ($M \pm SD = 5.82 \pm 1.11$) were slightly higher than for core DMN ($M \pm SD = 5.39 \pm 1.51$; $t(10321) = -16.87$, $p < .001$). These results suggest that while reading elicits more activation at the unimodal end of the gradient reflecting the importance of visual input in this task, both tasks elicit activation at the heteromodal apex of the gradient.

Effects of Conflict: Next, we characterised the main effect of task conflict in both Reading and Autobiographical memory trials, to identify brain regions responding to the presentation of distracting information (i.e. autobiographical memory cues on reading trials, or sentences on autobiographical memory trials). We did not find any conflict effects for reading. For autobiographical memory, the parahippocampus gyrus, temporal occipital fusiform, lateral occipital cortex, precuneus and anterior medial prefrontal cortex showed greater activation when there was no distracting sentence input (see Figure 7A), and these midline regions were identified as important areas for autobiographical memory by the *Autobiographical memory* > *Reading* contrast (see Figure 7C). Of those voxels that fell within DMN, 49% and 44% were within the core and medial temporal subnetworks within DMN, respectively, and 7% fell within the lateral temporal DMN subnetwork. In contrast, when there was conflict from irrelevant sentences during autobiographical memory recall, there was greater activation in regions that were also identified in *Autobiographical memory* > *Reading* contrast (see Figure 7C), including precentral gyrus, frontal pole, frontal orbital cortex, and angular gyrus (see Figure 7B), and also in regions that were

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identified as key sites for reading comprehension by the *Reading > Autobiographical Memory* contrast (see Figure 7D), including inferior frontal gyrus, superior/inferior/middle temporal gyrus, and visual cortex (including temporal occipital fusiform, and lateral occipital cortex; see Figure 7B). Of those voxels that fell within DMN, 90% were within the lateral temporal network within DMN, and 10% fell within the core DMN subsystem. These results suggest that the lateral temporal subsystem is more perceptually coupled, with stronger responses to presented sentences even when the required task was autobiographical memory. In contrast, the core DMN subsystem is more perceptually decoupled.

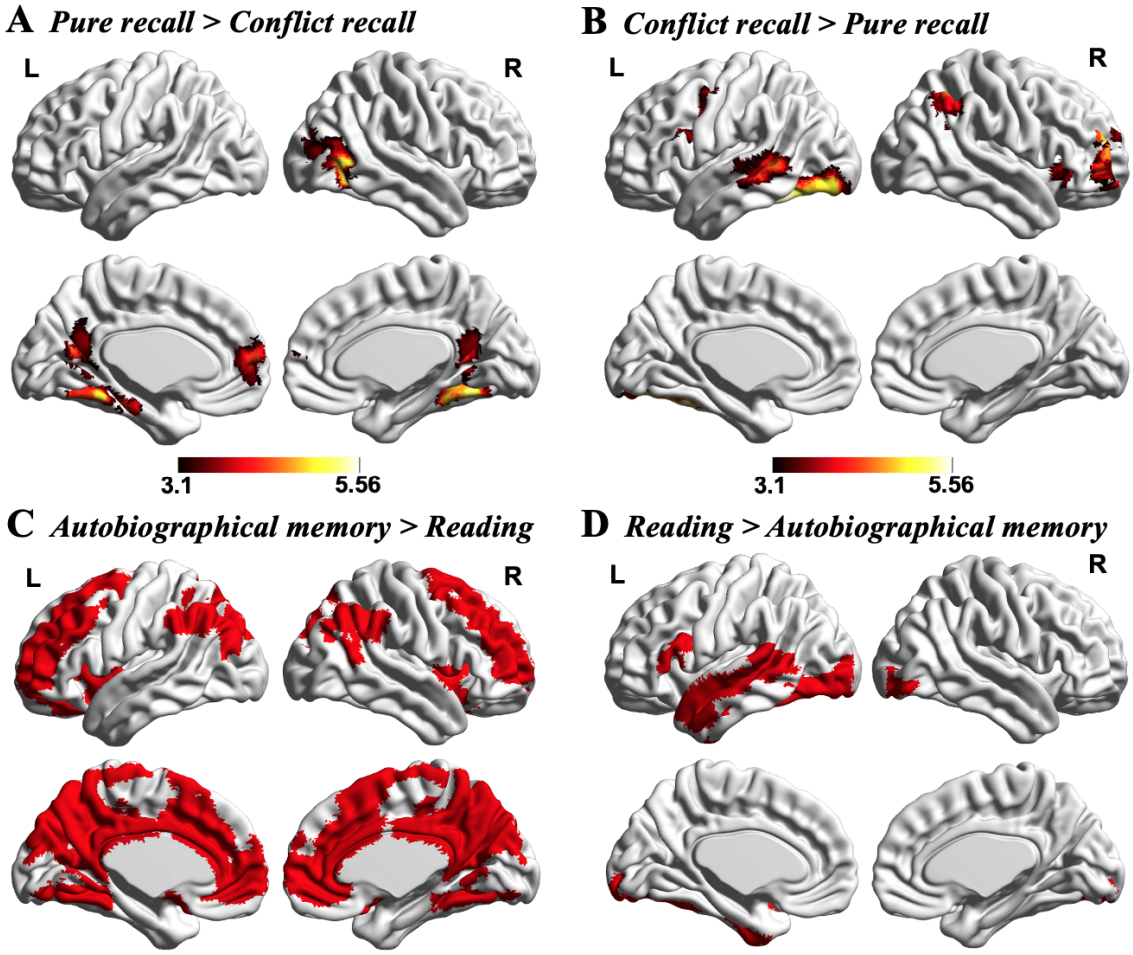

***Figure 7*. Effects of Conflict. A**) Significant activation when there was no conflict from semantic input defined using the contrast of *Pure recall > Conflict recall*. **B)** Significant activation when there was conflict from semantic input defined using the contrast of *Conflict recall > Pure Recall*. **C)** The midline regions showing greater activation to *Pure Recall* trials largely fell within areas identified as important for autobiographical memory. **D)** The stronger responses in lateral temporal cortex and visual cortex to *Conflict Recall* overlapped

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with regions identified as important for reading. All maps were thresholded at $z > 3.1$ ($p < .05$). L = Left hemisphere; R = Right hemisphere.

3.3.4. Parametric effects of task focus

Next, we examined the parametric effects of task focus in reading and autobiographical memory. Whole-brain parametric modelling revealed a stronger effect of task focus for autobiographical memory compared to reading in core DMN regions (including precuneus and medial prefrontal cortex), as well as in lateral occipital cortex and superior frontal gyrus (see Figure 8A).

When autobiographical memory was considered in isolation, greater task focus was associated with increased activation in frontal pole, superior frontal gyrus, medial prefrontal cortex, temporal fusiform cortex, precuneus, and lateral occipital cortex (Figure 8B). There was also greater deactivation in right angular gyrus (Figure 8C). More focussed autobiographical memory recall was therefore associated with greater activation of the medial temporal DMN subsystem plus a complex pattern of increased activation and deactivation in core DMN regions (see pie charts in Figure 8B-C). For reading, task focus was correlated with increased deactivation in regions associated with *Autobiographical memory* > *Reading* (including bilateral middle frontal gyrus, frontal pole, insular cortex, medial prefrontal gyrus, anterior/posterior cingulate gyrus, precuneus, and angular gyrus; Figure 8D). The areas within DMN mainly overlapped with the core subsystem. Overall, these results suggest that greater task focus in autobiographical memory recall is linked to activation in both medial temporal and core DMN subsystems, while deactivation of the same core DMN regions is linked to greater focus during reading.

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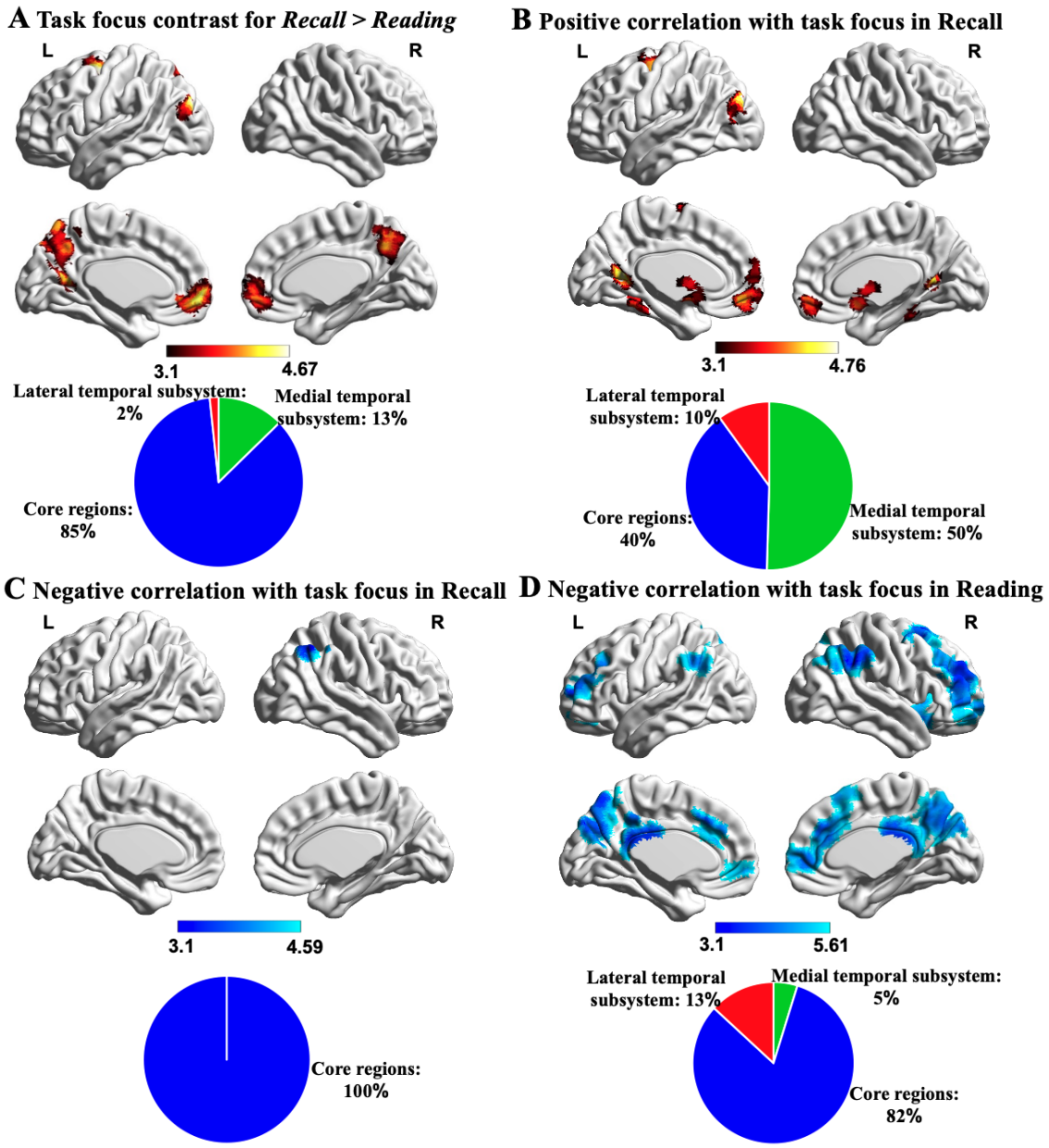

Figure 8. **Parametric effects of task focus. A)** The midline DMN core regions, lateral occipital cortex, and superior frontal gyrus showed greater task focus correlation effect for autobiographical memory recall. **B)** The midline DMN core regions, lateral occipital cortex and superior frontal gyrus showed stronger responses to better memory recall. **C)** Right angular gyrus showed increased activation when memory recall performance was poor. **D)** A wide range of regions that are important for autobiographical memory showed greater deactivation when people more focussed on reading. All maps were thresholded at $z > 3.1$ ($p < .05$). L = Left hemisphere; R = Right hemisphere.

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3.3.5. Psychophysiological interaction (PPI) analysis

We ran two PPI analyses, and all findings are Bonferroni corrected for two models. First, to understand how different networks are flexibly formed to support reading and autobiographical memory recall, PPI analysis examined patterns of functional connectivity for common semantic regions (the lateral temporal DMN subnetwork regions implicated in both tasks using a formal conjunction; see left panel in Figure 9A). This lateral temporal DMN conjunction seed showed greater connectivity with left inferior temporal gyrus (ITG), temporal occipital fusiform, and lateral occipital cortex (LOC) when comprehending sentences (corrected p = .001 see middle panel in Figure 9A), in regions previously identified by the *Reading* > *Autobiographical Memory* contrast. These regions do not overlap with DMN. The same lateral temporal DMN conjunction seed coupled with bilateral precuneus/posterior cingulate (corrected p < .001), anterior cingulate cortex (corrected p = .016), and left angular gyrus (corrected p = .028) during autobiographical memory recall (see right panel in Figure 9A), in regions previously identified by the *Autobiographical Memory* > *Reading* contrast. Of those voxels that fell within DMN, 91% were within core DMN regions.

Given that core DMN sites are thought to be critical to information transfer between subsystems (Andrews-Hanna *et al.* 2010; Andrews-Hanna, Saxe, et al. 2014), we also took the core DMN regions identified in the *Autobiographical memory* > *Reading* contrast map as a seed (see left panel in Figure 9B). During autobiographical memory recall, this site showed greater connectivity with left inferior frontal gyrus (corrected p = .006), left superior frontal gyrus (corrected p = .001), left middle temporal gyrus/lateral occipital cortex (corrected p = .014), and right middle temporal gyrus (corrected p = .014; see right panel in Figure 9B). A cluster in middle frontal gyrus did not survive Bonferroni correction for two models (corrected p = .09). Of those voxels that fell within DMN (for significant clusters), 98% fell within the lateral temporal DMN subsystem, and 2% were within core DMN. These results suggest that the lateral temporal DMN subsystem can couple with both visual areas and core DMN to support reading and autobiographical memory recall respectively. Meanwhile, core DMN can couple with lateral temporal DMN to support memory recall.

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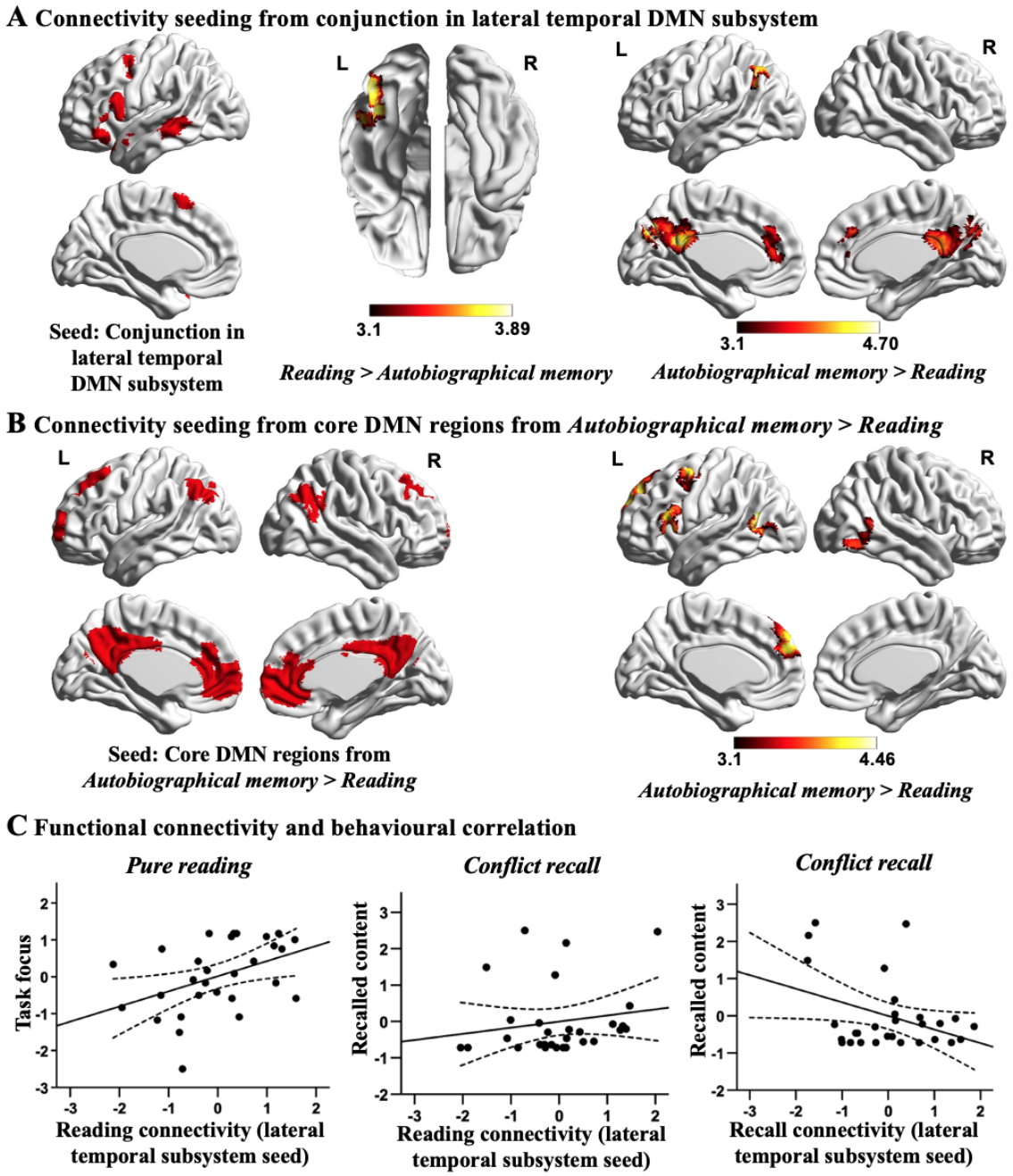

Figure 9. **Results of PPI analysis. A)** Patterns of significant connectivity between the lateral temporal DMN conjunction seed (in the left panel) and areas that are important for reading comprehension (in the middle panel) and other core DMN regions that are important for autobiographical memory (in the right panel). **B)** Patterns of significant connectivity between the core DMN seed (in the left panel) and areas that largely fell within lateral temporal DMN subsystem (in the right panel) during autobiographical memory recall. **C)** The scatterplots present the correlations between the PPI estimates of identified connectivity and task performance (i.e., task

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focus ratings inside the scanner and sentence recall performance outside the scanner) in each experimental condition. The error lines on the scatterplots indicate the 95% confidence estimates of the mean. Each point describes each participant. All maps were thresholded at $z > 3.1$ ($p < .05$). L = Left hemisphere; R = Right hemisphere.

We further tested for relationships between the strength of functional connectivity and behavioural performance (i.e., task focus ratings for reading and autobiographical memory trials and sentence recall outside the scanner). The PPI estimates were extracted from the clusters identified in *Reading* > *Autobiographical memory* and *Autobiographical memory* > *Reading* contrasts for each participant in each experimental condition. We then predicted behavioural performance in each condition with PPI estimates as covariates. Task focus ratings and sentence recall were included as dependent variables in *Pure reading*, *Conflict reading*, and *Conflict recall* conditions. For the *Pure recall* condition, only task focus ratings were relevant. For *Pure reading* and *Pure recall* with no conflict, only reading or recall connectivity were used as covariates, while for the two conflict conditions, both of these connections were included in the model. This analysis revealed that the strength of connectivity from the lateral temporal DMN seed to *Reading* > *Autobiographical memory* regions in the PPI was positively correlated with task focus in the *Pure reading* condition ($t(28) = 2.47$, $r = .41$, $p = .020$) and with sentence recall in the *Conflict recall* condition ($t(28) = 2.14$, $r = .37$, $p = .042$). The strength of connectivity from the lateral temporal DMN seed to regions *Autobiographical memory* > *Reading* regions in the PPI was negatively correlated with sentence recall performance in the *Conflict recall* condition ($t(28) = -2.70$, $r = -.47$, $p = .012$; see Figure 9C). There were no other significant correlations.

4. Discussion

This study provides a novel characterisation of the neural basis of perceptually-coupled and decoupled forms of cognition, and the effects of task focus in these contexts. Reading and autobiographical memory were sometimes set up in opposition, such that irrelevant autobiographical memory cues during reading could elicit the kinds of cognitive states that occur when our minds wander. Participants rated their task focus as it fluctuated across trials. Both reading and autobiographical memory elicited activation in

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the lateral temporal DMN subsystem, associated with semantic cognition, as well as in visual regions. Analysis of functional connectivity revealed the lateral temporal DMN subsystem was highly flexible, connecting more to visual regions during reading and to core DMN during autobiographical memory, and with these patterns of connectivity predicting performance and task focus. In addition, the tasks produced strikingly different patterns of deactivation relative to a low-level baseline task, with only reading eliciting deactivation within the DMN core subsystem, and neither task deactivating the lateral temporal subsystem. Importantly, there was a task-dependent relationship between core DMN deactivation and task focus: when participants were more focussed on the ongoing task, the core DMN subnetwork showed greater activation in autobiographical memory yet greater deactivation during reading. In contrast, the lateral temporal subsystem did not show effects of task focus and responded to visual inputs even when these were irrelevant to the task.

Despite clear, multi-dimensional differences between core and lateral temporal DMN subsystems, summarised in Table 2, the responses in these networks were found to fall at the same point on the principal gradient, which describes a cortical hierarchy from unimodal sensorimotor cortex to heteromodal areas of DMN. This allows us to reject the hypothesis that core DMN regions are nearer the top of the hierarchy by virtue of being more isolated from sensory inputs. Instead, the two DMN subsystems play distinctive and complementary roles in heteromodal cognition, with the lateral temporal subsystem supporting sensory integration and access to conceptual knowledge in both internally- and externally-oriented tasks, and core DMN supporting selective, task-dependent patterns of integration that support internally-oriented cognition.

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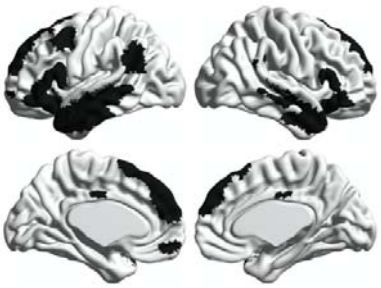
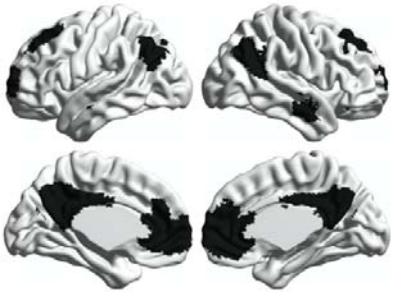
Table 2. *Summarisation of multi-dimensional differences between the lateral temporal and core DMN subsystems***.**

	Lateral temporal DMN subsystem	***Core DMN subsystem***
Dimensional differences		
Activation vs. deactivation	Activates across tasks; responds to task-irrelevant meaningful inputs	Task-specific patterns of activation and deactivation
Effects of task focus	No modulation of activation with task focus	Greater task focus accentuates task-specific patterns of activation and deactivation
Connectivity	Acts as a pivot, connecting to visual and core DMN regions	Varying connectivity to lateral temporal DMN regions
Hypothesised role in information integration	Semantic representation; visual access to heteromodal cortex	Selective integration; sustained internal cognition

Our finding that the lateral temporal DMN subsystem activates in response to both internal and external tasks that involve semantic cognition (i.e. reading and autobiographical memory) is consistent with prior work implicating lateral temporal cortex and inferior frontal gyrus in the representation and retrieval of heteromodal conceptual knowledge (Badre et al. 2005; Jefferies 2013; Noonan et al. 2013; Lambon Ralph *et al.* 2017). The task overlap in this DMN subnetwork was left-lateralised, in line with expectations for a semantic retrieval network (Noonan *et al.* 2013; Hurley et al. 2015; Rice et al. 2015; Gonzalez Alam et al. 2019; Jackson 2020). Previous studies have shown the engagement of lateral temporal cortex in both reading and memory recall (Svoboda *et al.* 2006; Ferstl et al. 2008; Summerfield et al. 2009; Andrews-Hanna, Saxe, *et al.* 2014; Lambon Ralph *et al.* 2017). Anterior and lateral temporal lobe

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regions are thought to provide a heteromodal semantic store, not strongly biased towards any one sensory input or feature type (Margulies *et al.* 2016; Lambon Ralph *et al.* 2017). This allows lateral temporal cortex to act as a "pivot" within the semantic system, forming distinct functional networks depending on the characteristics of the retrieval context (Chiou and Lambon Ralph 2019) – specifically, stronger connections to visual cortex when meaning must be extracted from visual inputs, and to core DMN regions when meanings are retrieved in the context of an internally-oriented task.

Other DMN regions in the core as opposed to the lateral temporal subnetwork are equally distant from sensory-motor regions along the principal gradient and yet show differences in their responsiveness to tasks. Chiou *et al.* (2020) suggested that core DMN regions show deactivation during externally-focussed tasks, while lateral temporal regions show engagement. We show that lateral temporal DMN activates in response to meaningful visual inputs (sentences versus letter strings), even when this input is irrelevant to the ongoing task, and irrespective of task focus. Consequently, this subnetwork may be able to detect situations in which meaning emerges in the environment, even when the focus of attention is elsewhere. In contrast, core DMN shows patterns of both increased activation or deactivation as participants report being more focussed, depending on the task. Fluctuating patterns of activation within core DMN may be crucial to our capacity to support both states such as autobiographical memory and mind-wandering, which are divorced from the environment in which they occur, and states such as reading comprehension which involve harnessing overlapping heteromodal regions to understand information in the environment.

DMN regions, across both core and lateral temporal subsystems, are implicated in information integration (Andrews-Hanna *et al.* 2010; Binney et al. 2012; Visser et al. 2012; Horner et al. 2015; Price *et al.* 2015; Bonnici et al. 2016; Lanzoni *et al.* 2020). Consequently, the divergent patterns of connectivity within DMN that we have described for reading and autobiographical memory might support distinct patterns of integration. In reading, a focussed pattern of cognition is required, centred on the meaning of words within their sentence contexts and their integration with long-term knowledge stores. In this context, semantic cognition needs to be partially insulated from other heteromodal codes also linked to DMN, which capture the individual's recent experiences, long-term episodic memories and current emotional state – all of which are irrelevant to the sentence being comprehended and which contribute to poor

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comprehension caused by mind-wandering. Deactivation of core DMN regions might achieve this selective pattern of integration. Individual differences in intrinsic connectivity between visual cortex, lateral DMN and core DMN regions have already been shown to relate to the ability to stay on task during reading, and avoid task-unrelated thoughts (Smallwood *et al.* 2013; Zhang *et al.* 2019). Greater task focus on reading was also associated with greater deactivation of regions in dorsolateral prefrontal cortex, anterior cingulate cortex, bordering pre-supplementary motor area, and right insula, associated with the ventral attention network. This pattern, although counterintuitive, is associated with participants focussing their thoughts away from their personal goals (Turnbull et al. 2019), potentially allowing attention to the external task.

In contrast, autobiographical retrieval is a multifaceted cognitive process that involves the retrieval of contextual details like sensory features, as well as pertinent semantic information and emotions (Conway 2001; Greenberg and Rubin 2003; Inman et al. 2018). This task is likely to require a broader pattern of integration across medial and lateral temporal subsystems, which are biased towards episodic and semantic retrieval respectively (Nyberg , McIntosh, *et al.* 1996; Nyberg, Mclntosh, et al. 1996; Badre and Wagner 2002; Jackson *et al.* 2016; Lambon Ralph *et al.* 2017). Core DMN might play an important role in this integration across domains, since core DMN regions showed greater activation during memory recall when there was no conflict from sentence presentation. Finally, we identified one DMN region in right AG that was negatively correlated with task focus in *both* reading and memory recall tasks. This site might be deactivated when attention is focussed on any specific task (Bzdok et al. 2013; Tyler et al. 2015), given that all tasks necessarily require a more focussed pattern of information integration than unconstrained thought in the absence of an externally-imposed task.

In conclusion, our study reveals distinct roles of lateral temporal and core DMN subsystems within cognition. The lateral temporal subsystem was activated by both internally- and externally-oriented tasks involving semantic retrieval, and as well as by meaningful inputs not relevant to the ongoing task, and this subsystem formed opposing task-specific functional networks. In contrast, core DMN regions showed task-specific patterns of activation and deactivation that were accentuated by increased task focus. We conclude the two DMN subsystems play distinctive and complementary roles in heteromodal cognition, with the lateral temporal subsystem supporting visual to conceptual knowledge, and core DMN supporting selective, task-dependent patterns of integration that support internally-oriented cognition. This

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division of labour might be key to our capacity to flexibly support different heteromodal mental states, which enables us to understand the world around us and also build internal thoughts that are independent from the immediate environment.

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Funding

This work was supported by the European Research Council (Project ID: 771863 – FLEXSEM to EJ and Project ID: 646927- WANDERINGMINDS to JS), and a China Scholarship Council (CSC) Scholarship (No. 201704910952 to MZ).

Declarations of interest

The authors have declared that no competing interests exist.

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Supplementary materials

Supplementary Analysis 1: Task activation

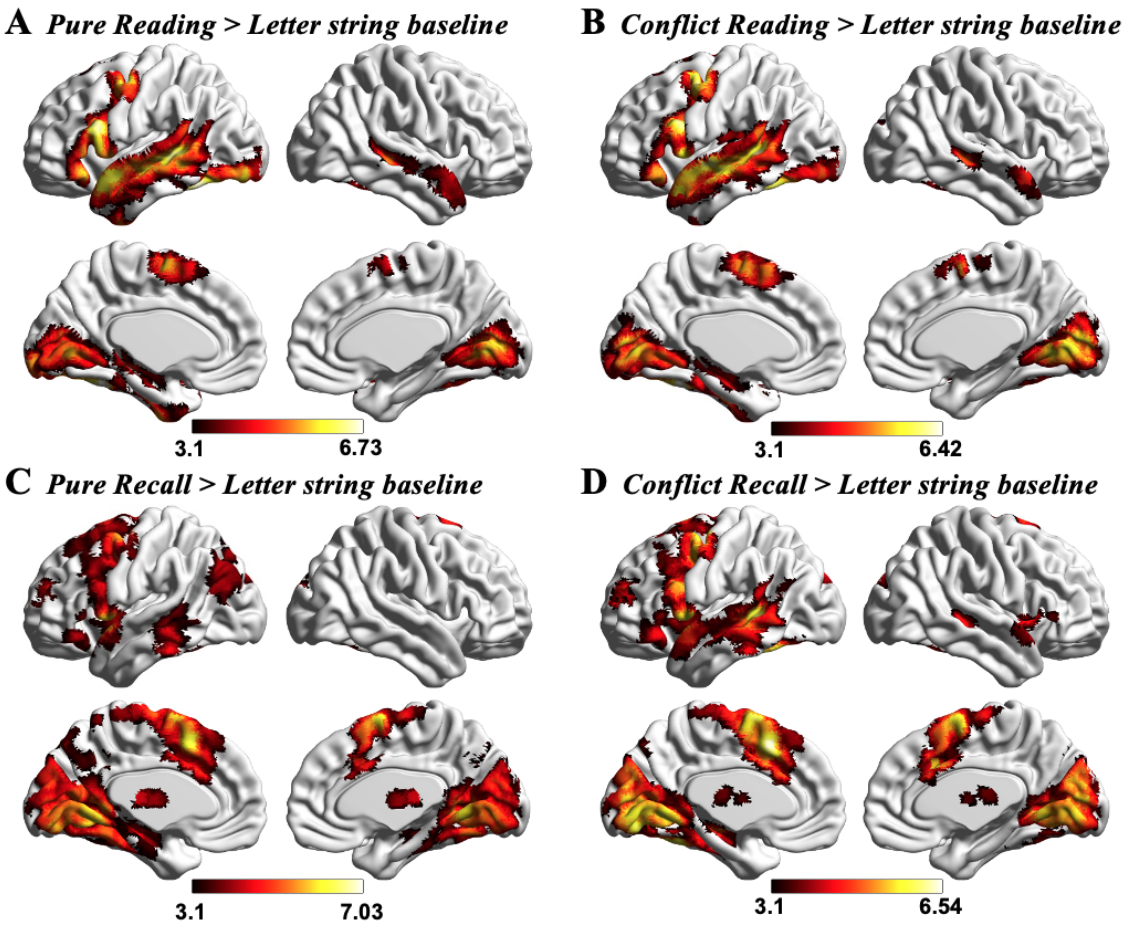

***Figure S1*. Comparisons between each experimental condition and meaningless letter string stimuli processing.** All maps were cluster-corrected with a voxel inclusion threshold of $z > 3.1$ and family-wise error rate using random field theory set at $p < .05$. L = Left hemisphere; R = Right hemisphere.

Supplementary Analysis 2: Gradient bin-by-bin analysis at threshold 2.3

A 2 (Activity: *Activation* vs. *Deactivation*) by 2 (Task: *Reading* vs. *Autobiographical memory*) by 10 (Bins) repeated-measures ANOVAs was conducted to examine the effect of Task in each bin at each state of activity. This three-way interaction effect was significant, $F(9,252) = 8.40$, $p < .001$, $\eta_p^2 = .23$, and separate ANOVAs analysis revealed that the interaction between Task and Bins was significant for both

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states of activity, with greater interaction effect in deactivation, $F(9,252) = 13.33$, $p < .001$, $\eta_p^2 = .32$, compared to activation, $F(9,252) = 2.90$, $p = .003$, $\eta_p^2 = .09$. Simple effects tests of the effect of Task in each bin at each state of activity revealed that the pattern of activation was similar between reading and autobiographical memory recall along the principal gradient (p values > .06 across all the bins: see Figure S2). However, reading elicited greater deactivation at the top of gradient relative to autobiographical memory (Bin 2, 4 - 10, p values < .004; see Figure S2), while comparable deactivation at the bottom of gradient (Bin 1and 3; p values > .06; see Table S1 for specific statistic reports). We observed the same patterns when replacing 0s with mean.

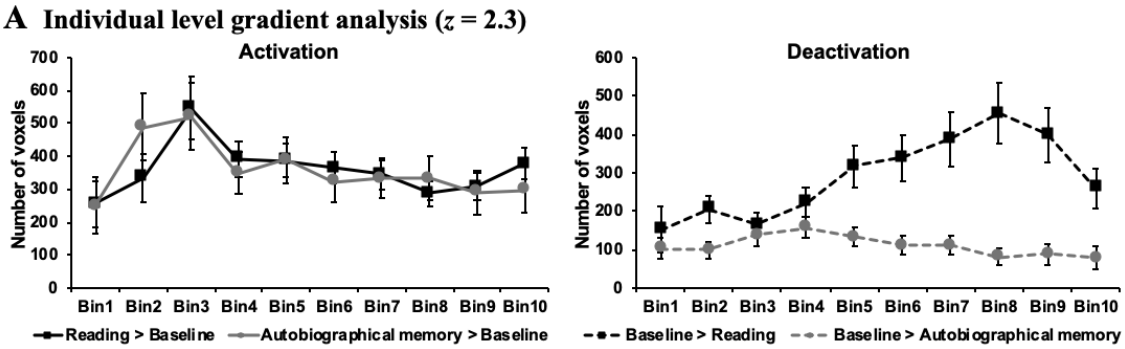

Figure S2. The whole-brain map was evenly divided into 10 bins from the bottom to the top of the gradient. The line charts present the activation and deactivation in each bin at each activity state relative to the letter string baseline. Error bars represent the standard error.

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Supplementary Analysis 3: Statistic reports of gradient bin-by-bin analysis

***Table S1*: Statistic reports of *t*-tests of gradient analysis at threshold 2.6 and 2.3.**

Bin	***z* = 2.6**		***z* = 2.3**	
	Activation	**Deactivation**	**Activation**	**Deactivation**
Bin 1	$t(28) = .55$, $p = .59$	$t(28) = 1.29$, $p = .21$	$t(28) = .17$, $p = .86$	$t(28) = 1.11$, $p = .28$
Bin 2	$t(28) = -1.78$, $p = .09$	$t(28) = 3.45$, $p = .002$	$t(28) = -1.99$, $p = .06$	$t(28) = 3.77$, $p = .001$
Bin 3	$t(28) = .73$, $p = .47$	$t(28) = .82$, $p = .42$	$t(28) = .36$, $p = .72$	$t(28) = 1.24$, $p = .23$
Bin 4	$t(28) = 1.64$, $p = .11$	$t(28) = 1.95$, $p = .06$	$t(28) = .93$, $p = .36$	$t(28) = 2.28$, $p = .03$
Bin 5	$t(28) = .79$, $p = .44$	$t(28) = 3.89$, $p = .001$	$t(28) = -.02$, $p = .99$	$t(28) = 4.18$, $p < .001$
Bin 6	$t(28) = 1.56$, $p = .13$	$t(28) = 4.21$, $p < .001$	$t(28) = .97$, $p = .34$	$t(28) = 4.55$, $p < .001$
Bin 7	$t(28) = 1.22$, $p = .23$	$t(28) = 4.25$, $p < .001$	$t(28) = .32$, $p = .76$	$t(28) = 4.60$, $p < .001$
Bin 8	$t(28) = -.31$, $p = .76$	$t(28) = 4.59$, $p < .001$	$t(28) = -.95$, $p = .35$	$t(28) = 4.93$, $p < .001$
Bin 9	$t(28) = .72$, $p = .48$	$t(28) = 4.19$, $p < .001$	$t(28) = .32$, $p = .75$	$t(28) = 4.66$, $p < .001$
Bin 10	$t(28) = 1.58$, $p = .12$	$t(28) = 3.15$, $p = .004$	$t(28) = 1.20$, $p = .24$	$t(28) = 3.42$, $p = .002$

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