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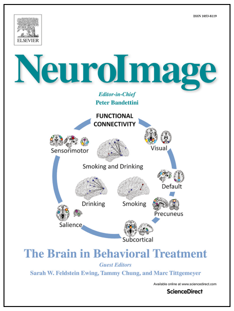

Individual variation in patterns of task focused, and detailed, thought are uniquely associated within the architecture of the medial temporal lobe

Nerissa Siu Ping Ho, Xiuyi Wang, Deniz Vatansever, Daniel Margulies, Boris Bernhardt, Elizabeth Jefferies, Jonathan Smallwood

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Title: Individual variation in patterns of task focused, and detailed, thought are uniquely associated within the architecture of the medial temporal lobe.

Authors: Nerissa Siu Ping Ho[a,*], Xiuyi Wang[a], Deniz Vatansever[b], Daniel Margulies[c], Boris Bernhardt[d], Elizabeth Jefferies[a] and Jonathan Smallwood[a].

Affiliations:

[a]Department of Psychology, University of York, England, UK.

[b]Institute of Science and Technology for Brain-inspired Intelligence, Fudan University, Shanghai, PR China.

[c]Centre National de la Recherche Scientifique (CNRS) UMR 7225, Institut du Cerveau et de la Moelle épinière, Paris, France.

[d]Multimodal Imaging and Connectome Analysis Lab, Montreal Neurological Institute and Hospital, McGill University, Montreal, Quebec, Canada

Address for correspondence:

Department of Psychology, University of York, England, UK.

E-mail address: nerissa.ho@york.ac.uk (N.S.P. Ho)

Abstract

Understanding the neural processes that support different patterns of ongoing thought is an important goal of contemporary cognitive neuroscience. Early accounts assumed the default mode network (DMN) was especially important for conscious attention to task-irrelevant / personally relevant material. However, simple task-negative accounts of the DMN are incompatible with more recent evidence that neural patterns within the system can be related to ongoing processing during active task states. To better characterise the contribution of the DMN to ongoing thought, we conducted a cross-sectional analysis of the relationship between the structural organisation of the brain, as indexed by cortical thickness, and patterns of experience, identified using experience sampling in the cognitive laboratory. In a sample of 181 healthy individuals (mean age 20 years, 117 females) we identified an association between cortical thickness in the anterior parahippocampus and patterns of task focused thought, as well as an adjacent posterior region in which cortical thickness was associated with experiences with higher levels of subjective detail. Both regions fell within regions of medial temporal lobe associated with the DMN, yet varied in their functional connectivity: the time series of signals in the 'on-task' region were more correlated with systems important for external task-relevant processing (as determined by meta-analysis) including the dorsal and ventral attention, and fronto-parietal networks. In contrast, connectivity within the region linked to subjective 'detail' was more correlated with the medial core of the DMN (posterior cingulate and the medial pre-frontal cortex) and regions of primary visual cortex. These results provide cross-sectional evidence that confirms a role of the DMN in how detailed experiences are and so provide further evidence that the role of this system in experience is not simply task-irrelevant. Our results also highlight processes within the medial temporal lobe, and their interactions with other regions of cortex as important in determining multiple aspects of how human cognition unfolds.

Keywords

Cortical thickness, default mode network, medial temporal lobe, parahippocampus, ongoing thought.

Highlights

Cortical thickness in regions of the medial temporal lobe (MTL) is linked to multiple features of ongoing thought.

Posterior MTL regions with close ties to the default mode network are associated with detailed experience.

Anterior MTL regions with links to task-positive systems are associated with degree of task-relatedness.

The MTL may be important in tethering default mode network processes to ongoing tasks.

1. Introduction

Humans spend almost one third of their lives engaged in patterns of thought focused on information other than the events taking place in the here and now (Killingsworth and Gilbert, 2010). Patterns of self-generated thoughts have psychological relevance since they are associated with a complex pattern of costs and benefits in daily life (Mooneyham and Schooler, 2013). Across individuals they are correlated with beneficial functions, such as intelligence (Turnbull et al., 2019), delaying gratification (Smallwood et al., 2013), and creativity (Agnoli et al., 2018; Baird et al., 2012; Fox and Beaty, 2018). They are also linked to more detrimental states such as rumination and unhappiness (Poerio et al., 2013; Ruby et al., 2013) and absentminded errors (Kane and McVay, 2012; McVay and Kane, 2009). As psychology is coming to terms with the different types of experience that constitute states such as mind-wandering (Seli et al., 2018), it becomes increasingly important to generate clear mechanistic accounts regarding how these distinct states emerge. Such attempts are often hampered due to methodological challenges encountered when trying to study patterns of cognition that are not driven by external input (Smallwood, 2013).

It is argued that measures of neural function can play an important role in bridging this gap, because they hold the potential to elucidate the underlying mechanisms that describe how different patterns of ongoing thought unfold (Christoff et al., 2016). Building on studies that examine ongoing thoughts from the perspective of individual differences, our study examined the association between cortical thickness, as measured by Magnetic Resonance Imaging (MRI), and patterns of ongoing thoughts recorded in the laboratory. Cortical thickness is a relatively stable neuroanatomical feature that is significantly influenced by genetic factors (Panizzon et al., 2009; Winkler et al., 2010) and closely associated with traits and neuropsychiatric disorders (e.g. Hardan et al., 2006; Rauch et al., 2005; Schilling et al., 2013). We hoped that by examining the correlation between whole brain cortical thickness and the patterns of experience that individuals report in the lab, we would be able to refine our understanding of the neural mechanisms that guide different aspects of ongoing thought.

1.1. Prior neurocognitive studies of ongoing experience

Within the field of cognitive neuroscience it was initially assumed that processing self-generated task-unrelated information during ongoing thought reflects the functioning of the so called 'default mode network' (DMN) - a constellation of regions encompassing the posterior and anterior medial cingulate, as well as lateral region in parietal and frontal cortex. This assumption was based on the tendency for the DMN to deactivate when participants engage in demanding external tasks (Raichle et al., 2001) as well as observations that activity in this system can be higher when (i) individuals report being off-task (Allen et al., 2013; Christoff et al., 2009; Stawarczyk et al., 2011) and (ii) during tasks that mimic the content of periods of task-irrelevant cognition, such as self-reference (e.g. Kelley et al., 2002; Macrae et al., 2004) and other forms of social cognition (e.g. Schilbach et al., 2008; Spreng and Grady, 2010).

However, recent work has highlighted the contribution of the DMN to cognition as broader than previously assumed. First, studies have suggested that the DMN may play a role in task relevant processing. For example, the DMN increases activity when participants perform simple tasks that depend on information from working memory (Konishi et al., 2015; Murphy et al., 2018a; Murphy et al., 2018b; Vatansever et al., 2018). It also shows functional coupling to task-positive regions in a manner that matches the demands of the external task (Krieger-Redwood et al., 2016; Vatansever et al., 2015). Other studies have shown that the DMN increases activity when individuals switch between different cognitive tasks, suggesting a role in generation and / or maintenance of task sets (Crittenden et al., 2016; Smith et al., 2018). (Crittenden et al., 2016; Smith et al., 2018). Finally, studies in the domain of memory processing have shown that the DMN is implicated in the levels of detail in both episodic (Bonnici et al., 2016; Richter et al., 2016) and semantic memories (Davey et al., 2015). Together these studies suggest the DMN may play an important role in task relevant processing, suggesting that conceptions of this network function as task-negative are unlikely to be correct.

Second, by recording neural activities while participants describe their ongoing thoughts, recent online experience sampling studies challenge accounts of the DMN as primarily contributing to off task states. For example, a study from our laboratory found neural activity within the DMN was linked, via representational similarity analysis, to the degree of detail in patterns of ongoing thought when participants were actively engaged in a working memory task (Sormaz et al., 2018). Similarly, Kucyi and colleagues (Kucyi et al., 2016) demonstrated that activity within regions of the DMN increases when behaviour is stable across time (see also Esterman et al., 2012). These lines of work indicate that the

DMN has an important role in patterns of ongoing thought, another strand of evidence demonstrating its function is broader than a simple role in task-irrelevant content.

Third, not only has recent work suggested that the DMN may contribute to elements of experience other than the off task state, there is also evidence that neural systems with a more well-defined role in task performance may be critical for maintaining focus on an external task. For example, a meta-analysis highlighted structures outside of the DMN, including the hippocampus, and dorsolateral prefrontal cortex, as important in studies exploring mind-wandering (Fox and Christoff, 2015). More recently, Wang et al. (2018a) used canonical correlation analysis to demonstrate that patterns of ongoing thought at rest corresponding to worrying current concerns were associated with reduced communication within neural systems important for external tasks (such as the dorsal and ventral attention network). This pattern was linked to poor performance on tasks of aptitude, suggesting links with problems in control anticipated by executive-failure accounts of off-task thinking (Kane and McVay, 2012; McVay and Kane, 2009). Together these data are consistent with the hypothesis that regions which play a general role in external task performance (e.g. the multiple demand network, Duncan (2010)) are likely to play an important role in patterns of ongoing thought by focusing attention on the task being performed.

1.2. Current study

Converging evidence from multiple domains, therefore, has brought into question the precise role the DMN plays in patterns of ongoing cognition. The current study was a cross-sectional investigation with the aim of understanding how different patterns of ongoing thought are linked to the structural organisation of the brain. Our study builds on our prior work that interrogated the neural correlates associated with individual variation in specific patterns of thought across large cohorts of individuals. In one of our prior studies (Smallwood et al., 2016), we used functional connectivity in a set of 80 participants to highlight that the DMN was important for many aspects of experience. Importantly, greater levels of detail was linked to functional connectivity between the parahippocampal gyrus and the posterior core of the DMN, while off-task thinking was linked to patterns of connectivity between lateral temporal cortex and the same region of posterior medial cortex. Further analysis of the same set of participants demonstrated that patterns of self-generated episodic content, but not off-task content, was linked to the white matter structure of the fornix and the connectivity of this region into the DMN core (Karapanagiotidis et al., 2017). Importantly, population level studies have shown the fornix is a critical white matter bundle that helps integrate neural signals from the hippocampus into the DMN core (Kernbach et al., 2018). In a second set of studies, using a larger cohort (n = 150), we used canonical correlation to show that spontaneous off-task thoughts can be distinguished from thoughts linked to vivid emotional experiences based on variance in the patterns of connectivity within the DMN core across individuals (Wang et al., 2018b). In the same cohort, examination of the whole brain functional connectivity of large scale networks also helped us identifying that patterns of on-task thinking were linked to the connectivity of the dorsal and ventral attention networks, rather than the DMN (Turnbull et al., 2019) – a finding that was consistent with investigation of patterns of thought at rest in a large open access data set described earlier (Wang et al., 2018a).

Building on these studies, our current study aimed to understand how individual differences in patterns of ongoing thought are related to cortical structure. In a smaller prior investigation (n = 40) we found cortical thickness within medial prefrontal regions of the DMN, as well as regions of anterior cingulate cortex in the ventral attention network were linked to greater off-task thought as measured in the laboratory (Bernhardt et al., 2014). This prior study only measured one dimension of experience (off-task thought) and it found that cortical thickness in the anterior cingulate and medial prefrontal regions were linked to off-task thought in situations when task demands were reduced. In the current study, we returned to this question regarding cortical structure and patterns of ongoing thought with a better optimised design. First, we had a much larger sample size (n = 181) which we hoped would ensure that we have sufficient power to identify true effects without the risk of a Type I error. Second, our current study included a measure of a greater variety of aspects of experience (see Table 1 for the experience sampling items that were used in this study). This facet of our design is important because it allows participants to describe more features of their ongoing experiences than is possible with single item measure of ongoing thought. In particular, our current study included items that described both task relatedness of experience, and features linked to subjective details (vividness and detail) so as to allow the chance to contrast views of the DMN as important for off-task states with an emerging view that it contributes to levels of subjective detail in experience. Third, we measured experiences in the laboratory across several days rather than in a single session. This ensured that we have a reasonably stable measure of ongoing thoughts that is, as far as possible, not influenced by short-term variations in cognition.

1.3. Specific analytic goals

Our first analysis related patterns of individual variation in ongoing thought to whole brain descriptions of cortical thickness, allowing us to determine how variations in cortical grey matter in different brain regions, link to different aspects of experience. Having determined these regions, we hoped to place these findings in a functional context using resting state data that was available for the majority of these participants. These resting state data were previously analysed with respect to patterns of ongoing thought by Turnbull et al. (2019) who used the functional connectivity of four canonical networks (dorsal and ventral attention, fronto-parietal and DMN) to measure dynamical changes in ongoing experience within a laboratory setting. In the current study, we analysed the resting state data to explore the functional architecture of cortical regions identified as related to different aspects of experience. We had two aims: (1) To determine if the patterns of functional connectivity associated with each region support potentially unique roles in ongoing thoughts and (2) To identify if the functional connectivity of these regions were also differentiated by variations in patterns of experience. Altogether we hoped this multi-modal neuroimaging approach would provide information on the role that different brain structures, and in particular those in the DMN, plays in ongoing cognition.

2. Material and methods

2.1. Participants

A group of 181 adults participated in the current study, all were healthy, right-handed, native English speakers, with normal or corrected-to-normal vision and no history of psychiatric or neurological illness. This cohort was acquired from the undergraduate and postgraduate student bodies at the University of York. For cortical thickness analysis, all 181 participants (female = 117), with average age of 20.2 years (range = 18-31, SD = 2.30) were analysed. These included 150 participants studied by Wang and colleagues (2018c) and Turnbull and colleagues (2019). For resting state functional connectivity analysis, the final sample was 165 participants (female = 105), with average age of 20.17 (range = 18-31, SD = 2.36). Eight participants were excluded due to missing or problematic imaging data, another nine were excluded because of excessive motion (see 2.5.2. Resting state fMRI Data – under Data preprocessing). As described in the introduction, aspects of the resting state data and their associations to patterns of ongoing thought have been previously published in various papers (Turnbull et al., 2019; Wang et al., 2018c).

All participants were volunteers who provided their written informed consent approved by the Department of Psychology and York Neuroimaging Centre, University of York ethics committees before commencement of any task and were debriefed after completion of the study. They were either paid or given course credit for their participation.

2.2. Procedures

Participants first arrived at the York Neuroimaging Centre to have their MRI images acquired in the scanner. There were no written instructions for the entire scanning protocol and participants were verbally instructed to look at the fixation cross and try not to sleep. Participants then took part in a comprehensive set of behavioural assessments that captured different aspects of cognition, including the experiential assessment task (see 2.3. Experiential assessment task) and other experimental tasks which were not analysed in the current study. These tasks were completed over two to three sessions on different days, with the order of sessions counterbalanced across participants. The tasks measuring ongoing experience always took place at the start of these laboratory sessions.

2.3. Experiential assessment task

The paradigm for measuring ongoing cognition was same as our recent studies (e.g. Sormaz et al., 2018; Turnbull et al., 2019), which is a variant of our earlier works (e.g. Karapanagiotidis et al., 2017; Smallwood et al., 2016). It manipulates memory load by using alternating blocks of 0-back (low-load) and 1-back (high-load) conditions, with the initial block being counter-balanced across individuals. The paradigm consisted of non-target trials, presented in runs of 2 to 8 with a mean of 5, followed by either a target trial or a multidimensional experience sampling (MDES) probe (see Figure 1). A black fixation cross (mean presentation duration = 1530 ms, 130 ms jitter) is presented in between trials. Participants were only required to make a behavioural response in target trials or MDES probes, but not in non-target trials.

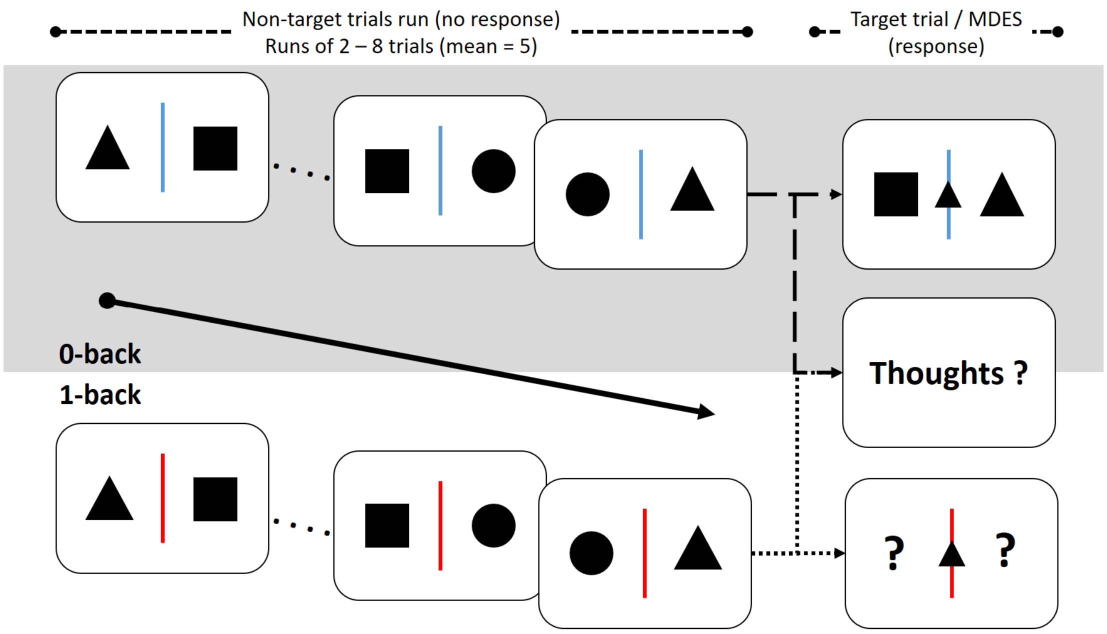

Figure 1. Experimental paradigm for measuring ongoing thought in the laboratory. Participants performed a simple visual decision making task in which they alternated between performing blocks when (i) the information required to make the discrimination was presented on screen (0-back, top) and (ii) when the same decision was made based on information from the prior trial (1-back, bottom). Non-target trials were identical across both task conditions, with black shapes (circles, squares or triangles) presented on either side of the screen and separated by a line (blue = 0-back; red = 1-back). Participants were only required to respond during target trials, by pressing a button to indicate whether the probe shape displayed on top of the centre line matched with the shape on the left or right hand side of the current (0-back) or previous (1-back) screen. Probes for assessing patterns of ongoing thought content, shown by the "Thoughts ?" prompt, appeared in 20% of the response trials in both task conditions to collect the multidimensional experience sampling (MDES) measures.

Non-target trials were identical across conditions, consisting of black shapes (circles, squares or triangles) separated by a line, the colour of which signified whether the condition was 0-back or 1-back (mean presentation duration = 1050 ms, 200 ms jitter). For target trials, participants were required to make a behavioural response by pressing a button, using a slightly different decision-making strategy depending on the condition. In the 0-back condition, there were a pair of black shapes presented on either side of a coloured line (indicating the condition) at the centre of the screen, with a probe shape displayed on top of the line. Participants had to press a button to indicate whether the probe shape matched the shape on the left or right hand side of the screen. In the 1-back condition, most of the presentation was the same except that instead of a pair of black shapes, there were two question marks presented on either side of the coloured line (also with the probe shape displayed on top of the line). Participants had to make similar responses as in the 0-back condition, but the decisions were based on whether the probe shape matched the shape on the left or right hand side of the screen on the previous (non-target) trial. Hence, only in the 1-back condition participants were required to maintain visuo-spatial information in working memory for each (non-target) trial in order to respond appropriately to the target trials. To provide a stable estimate of the participant's experience, several sessions of each task were performed on multiple days (range 2-3), with each session lasted around 25 minutes. The short session length was chosen to minimise time-on-task effect that has been shown to emerge as testing sessions extend beyond approximately 25 minutes (McVay and Kane, 2009). These effects were also expected to be limited in our task due to the low overall working memory load (Helton and Russell, 2011).

Finally, MDES was used to measure the contents of on-going thought during the 0/1-back task. On each occasion when participants were asked about their thoughts, they answered the 13 questions presented in Table 1. Participants always rated their level of task focus first and then described their thoughts at the moment before the probe on a further 12 dimensions. MDES probes occurred on a quasi-random basis to minimise the likelihood that participants could anticipate the occurrence of a probe. As explained above, at the end of each non-target trials run, participants were either probed with a target or, on 20% of the response trials, a MDES probe occurred.

Table 1: Multidimensional experience sampling questions

Dimensions	Questions	1	4
Task	My thoughts were focused on the task I was performing.	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
Person	My thoughts involved other people.	Not at all	Completely
Emotion	The content of my thoughts was:	Negative	Positive
Images	My thoughts were in the form of images.	Not at all	Completely
Words	My thoughts were in the form of words.	Not at all	Completely
Vivid	My thoughts were vivid as if I was there.	Not at all	Completely
Detailed	My thoughts were detailed and specific.	Not at all	Completely
Habit	This thought has recurrent themes similar to those I have had before.	Not at all	Completely
Evolving	My thoughts tended to evolve in a series of steps.	Not at all	Completely
Deliberate	My thoughts were:	Spontaneous	Deliberate

2.4. MRI data acquisition

All MRI data was acquired in a 3T GE HDx Excite MRI scanner using an eight-channel phased array head coil at the York Neuroimaging Centre, York. The protocol started with a structural scan based on a T1-weighted 3D fast spoiled gradient echo (TR = 7.8 s, TE = minimum full, flip angle= 20°, matrix size = 256 x 256, 176 slices, voxel size = 1.13 x 1.13 x 1 mm^3). It was followed by a nine-minute resting state fMRI scan using single-shot 2D gradient-echo-planar imaging (TR = 3 s, TE = minimum full, flip angle = 90°, matrix size = 64 x 64, 60 slices, voxel size = 3 x 3 x 3 mm^3, 180 volumes). Participants were requested to focus on a fixation cross in the middle of the screen throughout the resting state scanning.

2.5. Data preprocessing

2.5.1. Cortical thickness measurement

Cortical thickness was derived from the T1-weighted images using models generated by FreeSurfer (5.3.0; https://surfer.nmr.mgh.harvard.edu/), a tool widely validated on its accuracy of the thickness measures (Fischl, 2012) with histological analysis (Rosas et al., 2002), existing published thickness measures (Fischl and Dale, 2000; Von Economo, 1929) and manual measurements (Kuperberg et al., 2003). The processing pipeline (for details, please refer to Dale et al., 1999; Fischl et al., 1999), involved preprocessing steps of intensity normalization, removal of non-brain tissues, tissue classification, and surface extraction. This was followed by alignment of the extracted surfaces with curvature of an average spherical representation, fsaverage5, to improve the correspondence of locations across subjects. Finally, the cortical surface for each individual subject was visually inspected and manually corrected, if necessary, before cortical thickness was calculated, based on the closest distance between the grey/white boundary and pial surface at each vertex across the entire cortex. For whole-brain analysis, a surface-based smoothing with a 20 mm full-width-at-half-maximum (FWHM) Gaussian kernel was applied to reduce measurement noise without forgoing the capacity for anatomical localization (Lerch and Evans, 2005). This is a commonly used metric for both cortical and subcortical regions (Bernhardt et al., 2010; Bernhardt et al., 2014; Bernhardt et al., 2009; Valk et al., 2017).

2.5.2. Resting state fMRI Data

Preprocessing steps for the MRI data were carried out using the SPM software package (Version 12.0) (http://www.fil.ion.ucl.ac.uk/spm/) based on the MATLAB platform (Version 16.a) (https://uk.mathworks.com/products/matlab.html). After removing the first three functional volumes to account for the magnetisation equilibrium, the remaining data was corrected for motion using six degrees of freedom (x, y, z translations and rotations), and adjusted for differences in slice-time. Subsequently, the high-resolution structural image was co-registered to the mean functional image via rigid-body transformation, segmented into grey/white matter and cerebrospinal fluid probability maps, and were spatially normalized to the Montreal Neurological Institute (MNI) space alongside with all functional volumes using the segmented images and *a priori* templates. This indirect procedure utilizes the unified segmentation–normalization framework, which combines tissue segmentation, bias correction, and spatial normalization in a single unified model (Ashburner and Friston, 2005). Finally, all the functional images were smoothed using an 8 mm FWHM Gaussian kernel.

We have also applied the MRI data denoising procedure to remove potential confounds of motion and other artefacts, before performing the seed-based functional connectivity analyses (see Functional Connectivity Analysis in the Data Analysis Section below); and both of these steps were carried out using the *Conn* functional connectivity toolbox (Version 17.f) (https://www.nitrc.org/projects/conn) (Whitfield-Gabrieli and Nieto-Castanon, 2012). The denoising procedure was done by employing an extensive motion-correction procedure and denoising step, comparable to those reported in the literature (Ciric et al., 2017); and then entering the six realignment parameters and their second-order derivatives, a linear detrending term and the CompCor method that removed five principle components of the signal from white matter and cerebrospinal fluid (Behzadi et al., 2007) into the general linear model (GLM) (Friston et al., 1996) as covariates of no interest. At the same time, volumes with excessive motion were also identified and scrubbed based on the conservative settings of motion greater than 0.5 mm and global signal changes larger than z = 3, resulting in further exclusion for analysis of nine participants who had more than 15% of their data affected by motion (Power et al., 2014). Finally, a band-pass filter between 0.009 Hz and 0.08 Hz was employed in order to focus on low frequency fluctuations (Fox et al., 2005). As a result of the application of these procedures, the participants included for analysis had an average of 173.54 (range from 155 to 180) valid scans and an average denoising residual degrees of freedom of 60.28 (range from 52.4 to 63). Lastly, although recent reports suggest the ability of global signal regression to account for head motion (Power et al., 2017), it is also known to introduce spurious anti-correlations, and hence was not included in our processing steps (Saad et al., 2012).

2.6. Data analysis

2.6.1. MDES analysis

We employed principal components analysis (PCA) to these data to identify the unique patterns of variance associated with how the participants responded to these items. A complete description of the results of the analyses performed on these data are presented in Sormaz et al. (2018) and we summarised the results in Supplementary Table 1. In brief, we identified four reliable principal components that could be characterised as (i) 'Detail' - describing patterns of thought with the highest loadings on Detailed and Evolving, (ii) 'Off-Task' with low loadings on Task and Deliberate and higher loadings on Self, Future, Past and Person, (iii) 'Modality' with high loadings on images and low loadings on Words and (iv) 'Emotion' with strong loadings on Positive affect. Of these components identified, those during the harder 1-back condition, thoughts were more detailed, less off-task and more in the form of words than those in the easier 0-back condition. In addition, patterns of all components except ‘Emotion’ were consistent in weightings with a similar decomposition of a different data set in which a sample of the same individuals performed the same task while neural function was recorded using fMRI (Sormaz et al., 2018). Based on these four principal components obtained from the two conditions, eight scores were derived, namely four average scores across the two conditions and four difference scores across the two conditions (0-back less 1-back). We then calculated the corresponding z-scores and replaced outlying values (> 2.5) by the mean (percentage of outliners < 3.23%) before applying these values for further analysis.

2.6.2. Cortical thickness analysis

Cortical thickness data were analyzed using the SurfStat toolbox [http://www.math.mcgill.ca/keith/surfstat/] (Worsley et al., 2009). We entered all eight parameters associated with on-going thought contents (i.e., both average and difference scores calculated from 0/1 back task for each of the four principal components derived from MDES) into a single GLM in order to assess the effect of each of these parameters on cortical thickness at each vertex across the whole brain. Previous studies have established that both age (Fjell et al., 2009; Tamnes et al., 2009) and gender (Luders et al., 2006) have an effect on cortical thickness; consequently, these variables were also entered into the GLM model as covariates of no interest. Results were controlled for multiple comparisons using random field theory for non-isotropic images (Worsley et al., 1999), limiting the chance of reporting a family-wise error (FWE) at $p < .05$.

Finally, coordinates of the vertexes in each result cluster from cortical thickness analysis were extracted in MNI305 space and then transformed to NIfTI file in MNI152 space using 3dUndump command provided in AFNI (Analysis of Functional NeuroImages) (Cox, 1996). These clusters were subsequently used as the regions of interest (ROIs) for analysis of intrinsic connectivity measured using fMRI at rest.

2.6.3. Functional connectivity analysis

We used the resting state data to embed any regions identified through the cortical thickness analyses in a functional context and to understand whether the connectivity of these regions varied with individual differences in patterns of ongoing thought. Separate seed-based functional connectivity analyses were conducted based on the binarised seed

ROIs that were highlighted through the cortical thickness analyses. Individual connectivity maps for each participant were obtained by extracting the average BOLD signal within the time series of the ROI and then correlating these with the time courses from each individual voxel in the rest of the brain. These correlation results were then transformed to Fisher's Z-scores to produce the standardized functional connectivity, with positive and negative values indicating above and below average level of correlations respectively. Furthermore, to understand whether the functional connectivity of a given region varied with a particular type of experience, we entered the participants' PCA scores as explanatory variable into the model. Group-level inferences on positive and negative connectivity of the chosen seed ROIs were made based on one-sample t-tests. All reported clusters were corrected for multiple comparisons using a cluster threshold of $Z > 3.1$ (FWE corrected $p < .05$, uncorrected voxel-level $p < .001$). We also adjusted for Bonferroni correction of multiple comparison for the tests where separate models were examined for the same connectivity map (i.e., FWE threshold was set to $p < .025$ when two models were applied on the same connectivity map). The result brain networks were visualized using Connectome Workbench (v1.3.2). [https://www.humanconnectome.org/software/connectome-workbench]. In an attempt to rule out the possibility of excluding the effect of motion on spontaneous thoughts, we correlated the motion parameters with PCA scores for Detail and Off-Task thoughts and confirmed they had no significant correlations with both maximum (*Detail*: $r = .006$, $p = .942$; Off-task: $r = .045$, $p = .572$) and mean (Detail: $r = .127$, $p = .103$; Off-task: $r = .073$, $p = .350$) degree of motion.

2.6.4. Meta-analysis with NeuroSynth

Automated meta-analyses were conducted using NeuroSynth decoder (http://neurosynth.org/decode; Yarkoni et al., 2011) to make quantitative inferences on the results identified from the seed-based functional connectivity analyses. Unthresholded connectivity maps or ROI masks obtained from the functional connectivity analysis were submitted to NeuroSynth, which then computed the spatial correlations between each of these maps and every other meta-analytic map (n=11406) for each term/concept stored in the database (e.g., autobiographic, memory, task, emotional regulation). The top 15 meta-analytic words, excluding neuroanatomical terms, exhibiting the highest positive correlation with each connectivity map submitted were extracted and presented as wordclouds. Size of the font reflects the strength of the relationship, and its colour indicates the direction of the relationship (warm colours = positive and cooler colours = negative). This analysis allows us to quantify the reverse inferences that would be drawn from these functional maps by the larger neuroimaging community.

3. Results

3.1. Cortical thickness

Our first analysis was a group level regression in which spatial maps describing the whole brain cortical thickness for each individual were the dependent variables, and the eight measures that described individual participant's average and difference scores obtained during the two conditions in the 0/1-back task for each of the four MDES PCA components were included as explanatory variables (See Methods). This analysis revealed two clusters within the medial temporal lobe that were linked to individual variations in whether ongoing thoughts tended to be related to the task and how detailed they were, and another two clusters were linked to modality of their thoughts and how much the modality of thoughts change depending on the task demand. The clusters are presented in Figure 2 and Figure 8 respectively (See section 3.2.2. Modality of experience for more descriptions of the second part of these findings). Cortical thickness in a more posterior region was linked to greater levels of detail, while the more anterior region was related to greater on-task focus (i.e. negatively correlated with off-task content). It can be seen in the left hand panel in Figure 2 that both regions fall within a region of the medial temporal lobe that is allied to the DMN as defined by Yeo and colleagues (2011). No significant whole brain patterns were reliably associated with task differences in either detail or on-task thought. We performed a post-hoc analyses to ensure that the inclusion of all the PCA scores in a single model could have obscured particular brain-experience that would have otherwise been observed if each component was included in a separate model. To ensure that this was not the case, we repeated the cortical thickness analysis using separate models for both Detail and On-task components. This revealed almost identical results (see Supplementary Figure 1).

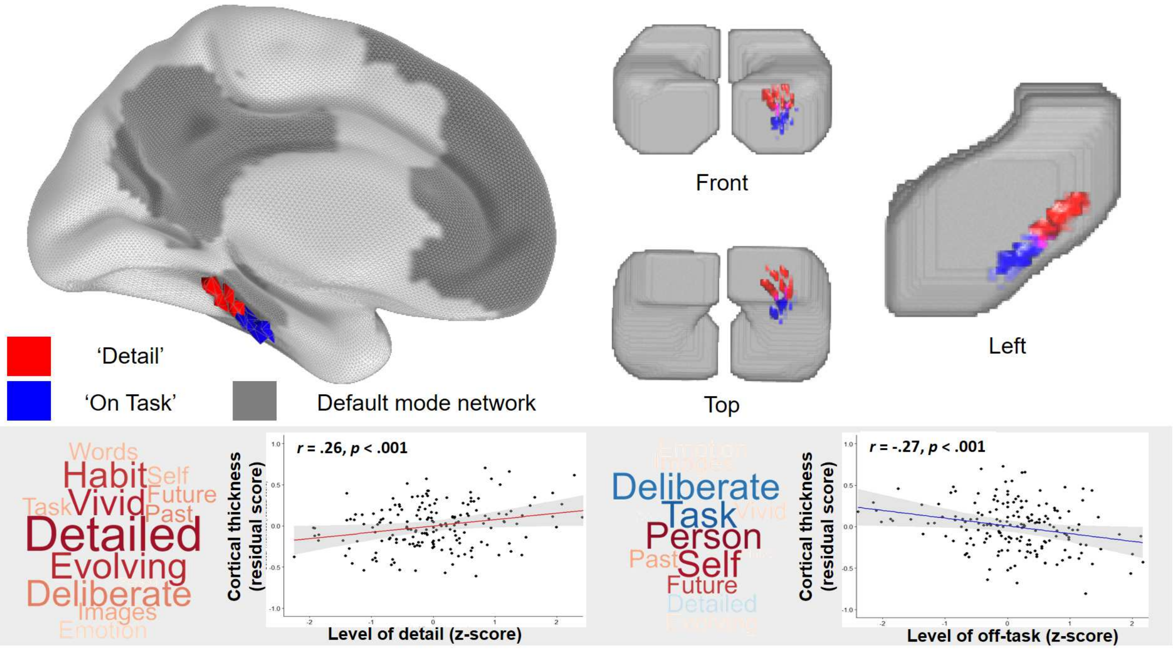

Figure 2. Adjacent regions of the parahippocampus that show distinct relationships to two types of ongoing experience (task-relatedness, blue, and detail, red). For the purpose of comparison, the default mode network is displayed in black on the left hand brain. The word cloud highlights the loading on the principal component with the size of the font highlighting the strength of the relationship, and the colour indicating the direction of the relationship (warm colours = positive and cooler colours = negative). The scatterplots show the relationship of cortical thickness and level of detail / off-task in thoughts for individual participants.

3.2. ***Functional connectivity***

3.2.1. Detail and on-task experience

Our first analysis highlighted adjacent regions within the medial temporal lobe that show correlations between cortical thickness and different aspects of experience across individuals. Next, we used seed-based functional connectivity applied to resting state data in order to embed these regions within a functional context (see 2.6.3. Functional connectivity analysis under Data analysis). In particular, given the spatial proximity of both clusters identified by our analysis, we hoped to address whether the two regions differed in their connectivity in either quantitative manner (i.e. patterns of functional connectivity that do not vary in the spatial distribution but in their intensity) as well as in a qualitative manner (i.e. patterns of connectivity with different spatial distribution).

To identify 'quantitative' differences in the pattern of connectivity between the two regions of the parahippocampus, we first generated maps describing the spatial distribution of both increased and decreased functional connectivity for each seed for each participant (See Supplementary Figure 2), and then created two spatial conjunctions, one for positive correlations (regions with above average connectivity with both seeds) and the other for negative correlations (regions with below average connectivity with both seeds), to identify common regions within these maps. The combined results of these two analyses are presented in the left hand panel of Figure 3 where it can be seen that both seeds showed increased connectivity to regions of the default mode and visual network, and decreased connectivity to regions that broadly corresponded to the ventral attention network. Meta analytic decoding of these regions highlighted terms linked to autobiographical memory for regions with positive connectivity, and pain and inhibition for regions with relatively lower connectivity to both seed regions. Furthermore, we examined whether there were quantitative differences in the connectivity between the seed maps within these common regions by extracting parameter estimates that describe their associations with each region of the parahippocampus and comparing these using a paired t-test. Significant seed differences were observed for both regions showing positive ($t(164) = 11.59$, $p < .001$) and negative connectivity ($t(164) = -4.41$, $p < .001$). These data are plotted as bar graphs in Figure 3, where it can be seen that the posterior region of the parahippocampus was more positively coupled with regions showing positive connectivity with both seeds, while the anterior region was less negatively correlated with regions that were generally less negatively coupled with both regions (see Supplementary Figure 3 for a cluster by cluster breakdown of the data and Supplementary Table 2 for the full list of clusters).

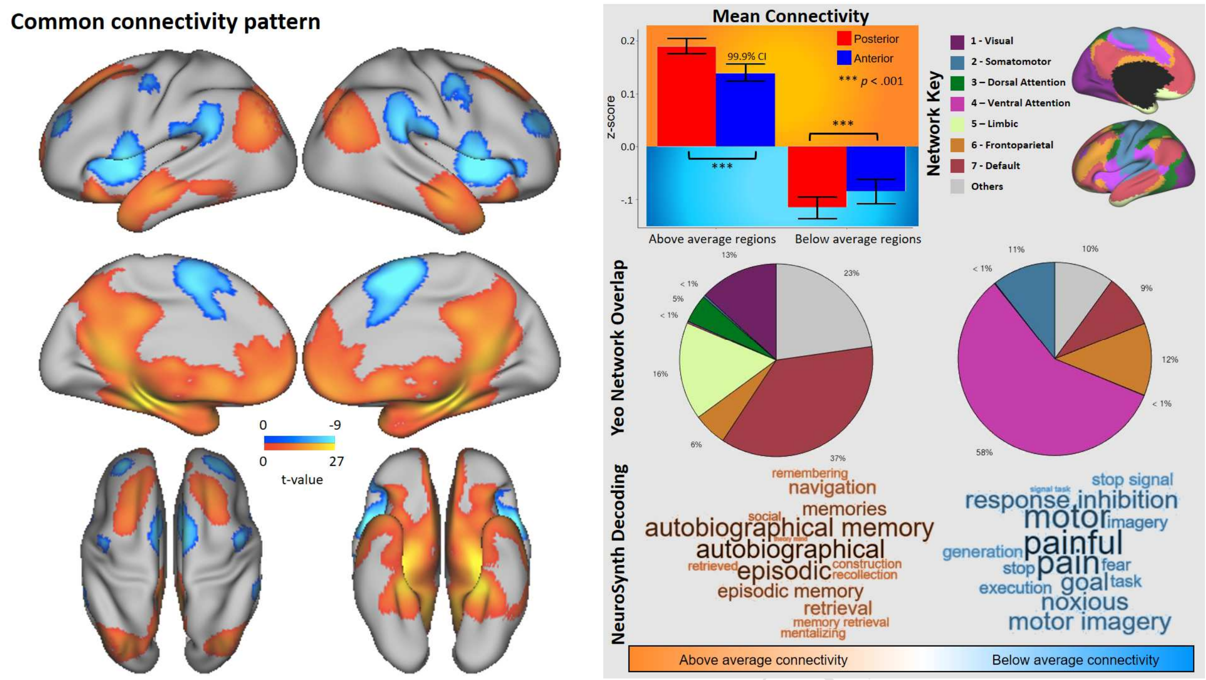

Figure 3. Brain regions showing common connectivity with anterior and posterior parahippocampal gyrus. (Left): Regions in orange-yellow show above average connectivity with both the posterior and anterior regions of the parahippocampus. Regions in blue-lightblue show areas with lower than average connectivity to both parahippocampal seeds. All images thresholded at $Z = 3.1$, $p < .05$ (corrected for familywise error). (Right): The bar graphs represent the standardized mean connectivity of each seed for regions showing common connectivity (red=posterior, blue=anterior). The pie charts highlight the percentage of voxels within each connectivity map fall within each of the seven large scale networks identified by Yeo et al. (2011). The colour scheme used in the pie chart shows the correspondence to Yeo Seven network parcellation and is also presented in the Network Key. The word clouds highlight the items most associated with the respective patterns of connectivity based on a NeuroSynth meta-analysis. Items with a larger font size indicated stronger association. All anatomical terms have been removed.

The analysis presented in Figure 3 demonstrates that regions showing common connectivity with both regions of the parahippocampus identified through our cortical thickness analysis show quantitative differences in the strength of their connectivity. Our next analysis examined whether there are also regions of cortex that exhibit qualitative differences in their relationships to the parahippocampal seeds. To address this possibility we generated a mask that contained all of the regions of cortex that exhibited either common positive and negative correlations with both seeds (i.e. the spatial maps in Figure 3). Next for each participant we calculated the differential connectivity between posterior and anterior parahippocampus and the rest of the cortex. Finally, we performed a group level analysis on these maps using the common positive and negative regions as an exclusive mask. We focused on the four largest positive and negative clusters in the cortex (see Supplementary Table 3 for the full set of the clusters). Figure 4 shows the results of this analysis which identified a distributed network of regions showing differential connectivity with both seeds. Figure 5 and 6 shows the specific connectivity with each region on a cluster by cluster basis.

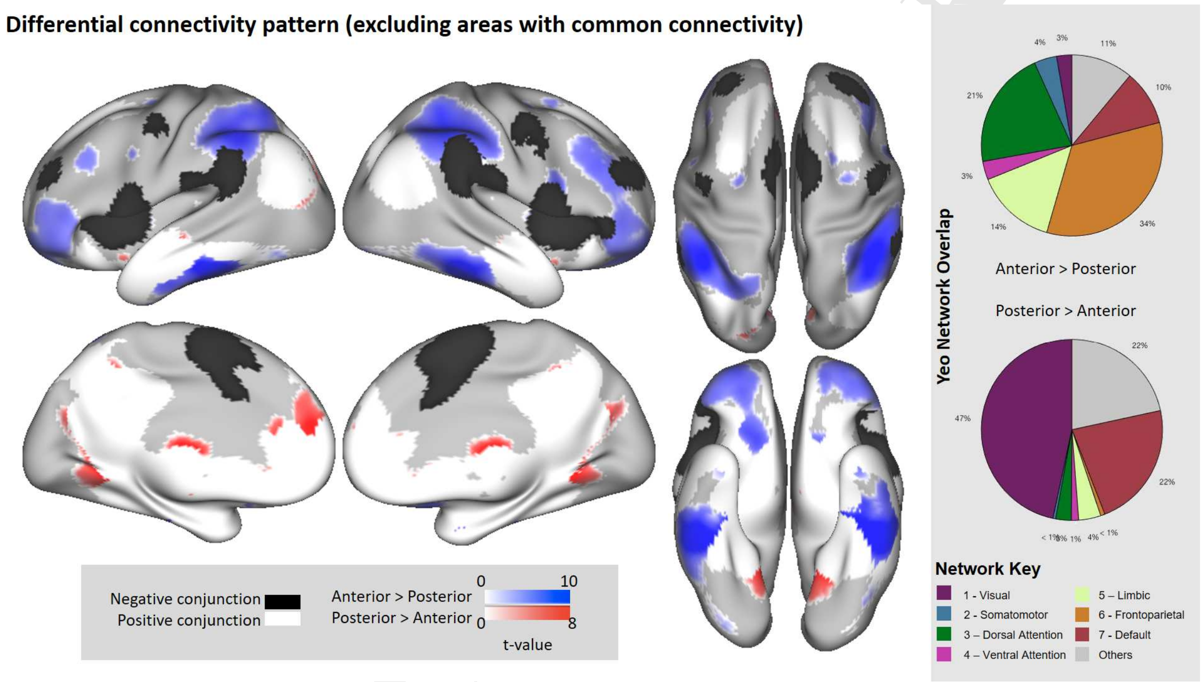

Figure 4. Brain regions showing differential connectivity (after excluding areas with common connectivity) with anterior and posterior parahippocampal gyrus. (Left): Regions in red show stronger coupling to the posterior seed while regions in blue are more strongly coupled to the anterior seed region, excluding regions in the conjunctions map shown in black and white. All images thresholded at $Z = 3.1$, $p < .05$ (corrected for familywise error). (Right): The pie charts highlight the percentage of voxels within each connectivity map fall within each of the seven large scale networks identified by Yeo et al. (2011). The colour scheme used in the pie chart shows the correspondence to Yeo Seven network parcellation and is also presented in the Network Key.

Notably, the regions identified as more correlated with the posterior seed tended to show greater above average connectivity (see Figure 5). The largest cluster that is within the visual network (Yeo 1), and two of the other clusters are in the DMN (Yeo 7). In contrast, regions more closely aligned to the anterior region tended to show lower than average connectivity with the posterior region but not with the anterior region (see Figure 6). One exception to this was a large cluster that included both the right dorsolateral prefrontal cortex (Yeo 6) and the limbic area (Yeo 5) which showed above average connectivity with the anterior but not the posterior parahippocampus seed.

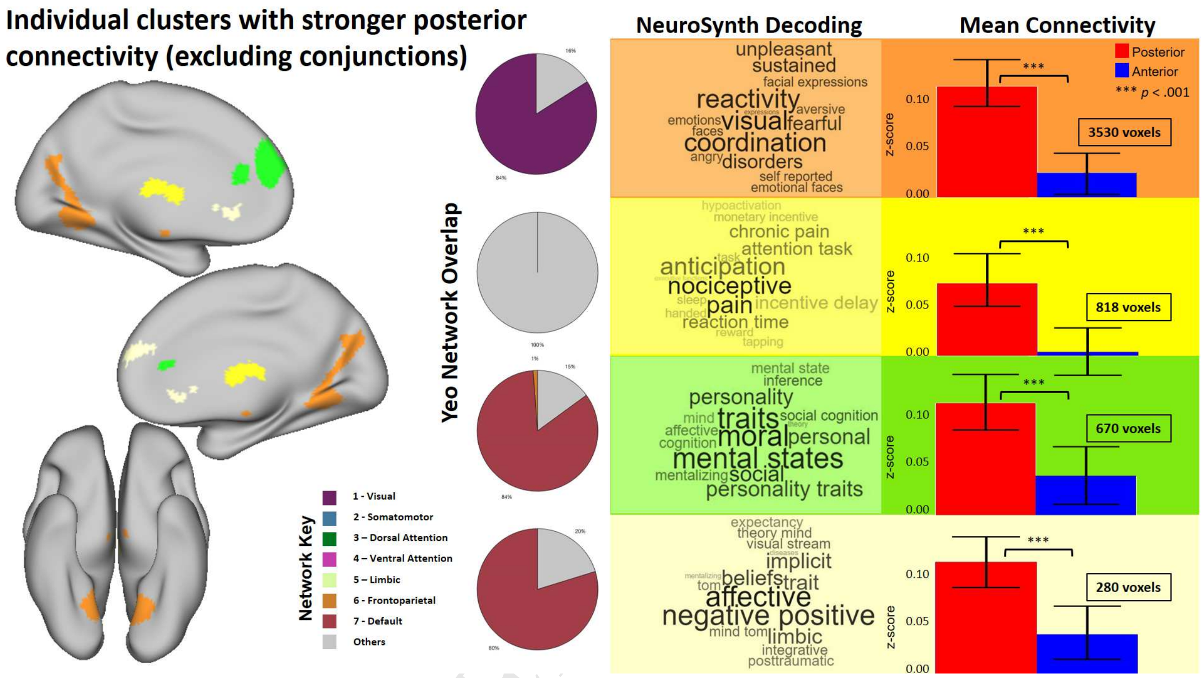

Figure 5. Individual clusters showing stronger coupling to the posterior seed (after excluding areas with common connectivity). (Left): Individual clusters showing stronger coupling to the posterior seed are highlighted in different colors. All images thresholded at Z = 3.1, p < .05 (corrected for familywise error). (Middle-Left): The pie charts highlight the percentage of voxels within each connectivity map fall within each of the seven large scale networks identified by Yeo et al. (2011). The colour scheme used in the pie chart shows the correspondence to Yeo Seven network parcellation and is also presented in the Network Key. (Middle-Right): The word clouds highlight the items most associated with the respective patterns of connectivity based on a NeuroSynth meta-analysis. Items with a larger font size indicated stronger association. All anatomical terms have been removed. (Right): The bar graphs represent the standardized mean connectivity of these clusters at 99.9% confidence interval (background color of the bar graphs indicates the same colored cluster it corresponded) in the two seed maps (red=posterior, blue=anterior).

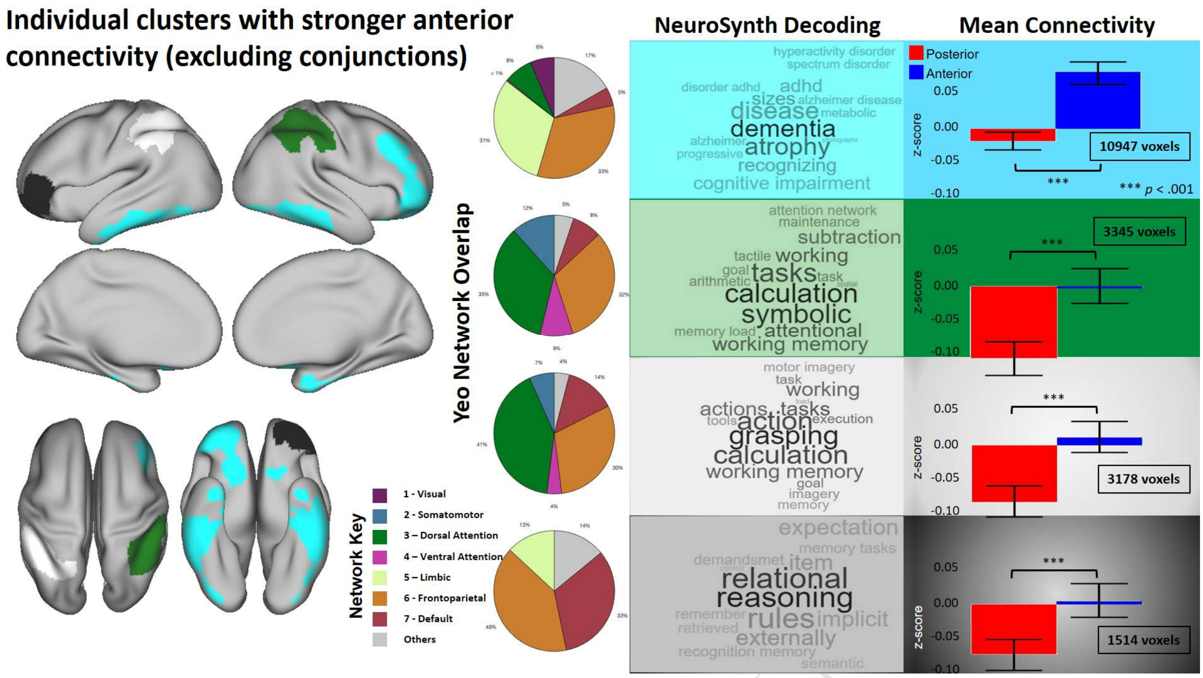

Figure 6. Individual larger clusters showing stronger coupling to the anterior seed (after excluding areas with common connectivity). (Left): Individual clusters showing stronger coupling to the posterior seed are highlighted in different colors. All images thresholded at Z = 3.1, *p* < .05 (corrected for familywise error). (Middle-Left): The pie charts highlight the percentage of voxels within each connectivity map fall within each of the seven large scale networks identified by Yeo et al. (2011). The colour scheme used in the pie chart illustrates the correspondence to Yeo Seven network parcellation and is also presented in the Network Key. (Middle-Right): The word clouds highlight the items most associated with the respective patterns of connectivity based on a NeuroSynth meta-analysis. Items with a larger font size indicated stronger association. All anatomical terms have been removed. (Right): The bar graphs represent the standardized mean connectivity of these clusters at 99.9% confidence interval (color scheme used for the background of the bar graphs corresponds to the color scheme of the clusters shown in the brain on the left) in the two seed maps (red=posterior, blue=anterior).

Together our analyses suggest the two regions of the parahippocampus that are linked to different forms of experience were also distinguished by their functional connectivity in both quantitative and qualitative terms. Relative to the anterior region of parahippocampus, the posterior region was more positively correlated with regions that had above average correlation with both regions (core regions of the DMN and visual system). Posterior parahippocampus also had reduced connectivity with regions of the ventral attention network that exhibited weaker correlations with both seeds. Furthermore, there were regions identified with more ‘qualitative’ differences in their patterns of functional connectivity. For example, a cluster encompassing the right dorso-lateral prefrontal cortex was identified with above average connectivity with the anterior but not posterior parahippocampus. Similarly, regions of both dorso medial prefrontal cortex, within the DMN, and a region of temporo-occipital cortex, within the visual network, had above average correlation with the posterior while connectivity was close to baseline levels for the anterior parahippocampus.

So far our findings indicate that cortical thickness at different regions in the medial temporal lobe may reflect variations in both the level of detail in experience, as well as their level of task focus. These different regions of parahippocampus form differential connections with other regions in the cortex which may explain why they relate to different aspects of experience. Our final analysis examines whether differences in the connectivity of these two parahippocampal regions also varies with individual differences in the relative aspects of experience. To explore this possibility, we performed a group level regression in which spatial maps describing the difference in connectivity between the posterior and anterior regions was the dependent variable. The average PCA scores for detail and off-task for each person were entered as explanatory variables (see 2.6.3. Functional connectivity analysis under Data analysis).

This analysis revealed two regions within the right lateral parietal and frontal cortex with stronger connectivity with anterior than posterior regions for individuals who were more ‘on-task’. These regions both fell with areas of cortex that had above average connectivity with both regions of the parahippocampus. We also found a region of left ventral lateral prefrontal cortex with a reverse pattern, it was more correlated with posterior than anterior for individuals who were ‘on-task’. This region fell within a region that had below average connectivity with both regions of the parahippocampus. These regions are presented in Figure 7. No significant results were observed for variation in detailed thought.

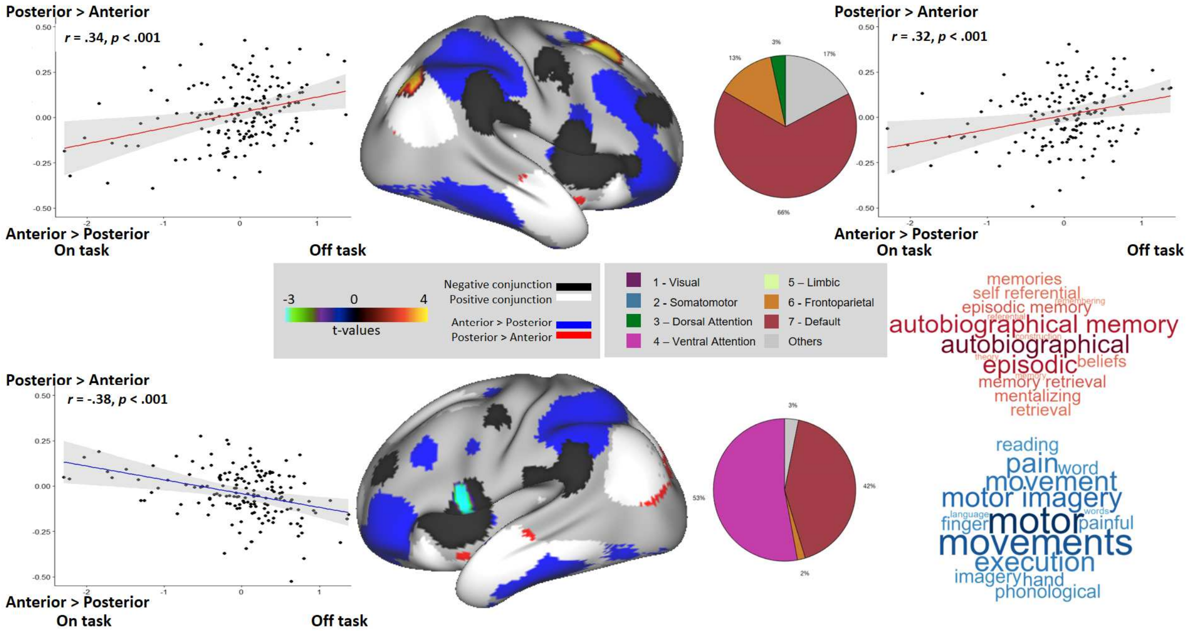

Figure 7. ***Clusters with differential connectivity between the two parahippocampus seeds being modulated by the patterns of off-task thought.*** Differential connectivity between the two parahippocampus seeds are shown to be modulated by patterns of off-task thoughts. The pattern of correlation for each seed are shown in the corresponding scattered plots. All images thresholded at Z = 3.1, *p* < .05 (corrected for familywise error). The pie charts highlight the percentage of voxels within each connectivity map fall within each of the seven large scale networks identified by Yeo et al. (2011). The colour scheme used in the pie chart shows the correspondence to Yeo Seven network parcellation and is also presented in the Network Key. The word clouds highlight the items most associated with the respective patterns of connectivity based on a NeuroSynth meta-analysis. Items with a larger font size indicated stronger association. All anatomical terms have been removed.

To provide further insight into interpreting these patterns of modulated functional connectivity, we calculated their spatial relationship with respect to canonical large scale networks. Regions in both the parietal and frontal lobe spanned across both regions of the DMN (69%) and fronto-parietal network (13%) (Figure 7), while the ventral lateral cortex fell within both the ventral attention network (53%) and the DMN (42%).

Taken together, these findings suggest that individual variation in task focus may emerge from a trade-off in the connectivity of the regions of medial temporal lobe identified through our cortical thickness analysis. In particular, individuals who maintain better task focus tend to show (a) relatively stronger connectivity between anterior regions of the medial temporal lobe with regions of cortex that show connectivity that is common to both seeds and that falls within regions of the default mode and fronto-parietal networks and (b) relatively stronger connectivity between posterior medial temporal regions and regions of lateral prefrontal cortex that shows patterns of reduced connectivity with both anterior and posterior seeds.

3.2.2. Modality of experience

As discussed above, our initial cortical thickness analysis also revealed two additional results associated with the component describing the modality of ongoing thoughts. Cortical thickness in a region of dorsal precuneus was associated with experiences characterised as words, while a region of ventral motor cortex in the right hemisphere was associated with whether individuals varied the modality of their experiences with respect to the task in hand. These results are presented in Figure 8. Both regions showed a pattern of strong connectivity with visual and sensorimotor regions (Yeo 1 and 2) and strong anti correlation with the DMN (see Supplementary Figure 4). These spatial maps are similar to the principle gradient identified by Margulies et al. (2016). These results were not the focus of our analysis and we consider their possible significance for our understanding of how neural processes are able to support different modalities of ongoing thought in the Discussion.

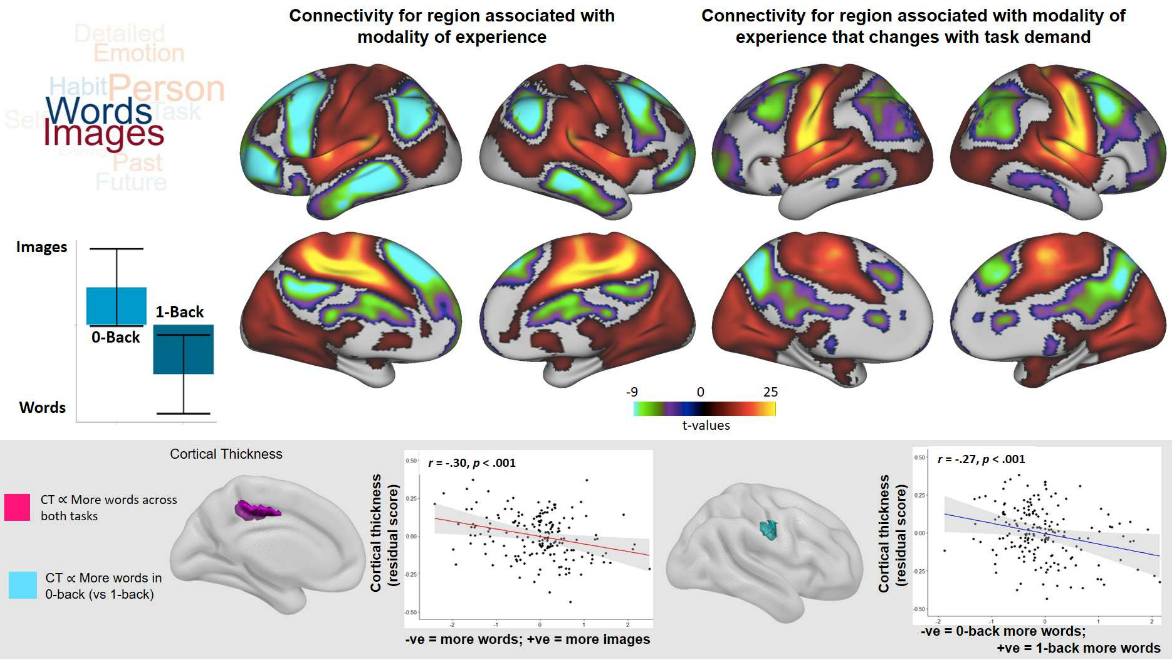

Figure 8. Regions of cortex where cortical thickness is associated with the modality of ongoing experience, and how it changes with task demands (bottom) and their associated functional connectivity maps (top).

4. Discussion

Using multiple imaging methods in a large cohort of individuals, our study identified adjacent regions within the medial temporal lobe that are linked to different patterns of experience, both of which fall within the DMN. The most direct evidence of a role for this large scale system in ongoing cognition comes from the posterior region of the parahippocampus, which we found predicted reports of detailed cognition, a type of thinking that is elevated in the more demanding condition of the task in which we assessed ongoing experience (Sormaz et al., 2018; Turnbull et al., 2019). This region had relatively strong connections into the core of the DMN, as well as with regions visual cortex. These data add to a growing body of evidence that regions within the DMN may contribute to the level of subjective detail in experience. In our prior online experience sampling studies using the same task paradigm, we found neural signals within the DMN were associated with online patterns of detailed task-relevant cognition (Sormaz et al., 2018). In addition, Makovac and colleagues (Makovac et al., 2017) found that reports of detail in ongoing thoughts were linked to decoupling between regions of the DMN and the amygdala in both patients with anxiety and controls. Gorgolewski and colleagues (2016) found that at rest, higher low frequency fluctuations within a right parietal cluster extending into the angular gyrus aspect of the DMN was associated with patterns of ongoing thought with more specific details. There are other studies that provide support for our finding that the medial temporal lobe may be important in determining levels of subjective detail. For example, in a sample of well-trained meditators, activity within regions of the hippocampus was linked to descriptions of experience as evolving (Ellamil et al., 2016), a pattern which may be relevant to our study given that the ‘Detail’ component from our analysis is also characterised by descriptions of experience as evolving. In addition, patients with lesions in the hippocampus reported comparable levels of off-task thought, but these experiences were generally lacking rich episodic details (McCormick et al., 2018). Similarly, structural abnormalities in the posterior cingulate that emerge in dementia contribute to deficits in the level of detail in memories (Irish et al., 2014) and problems in generating vivid scenes in imagination (Irish et al., 2015). Finally, a role for the DMN in the level of detail in ongoing cognition is consistent with studies showing similar contributions in tasks that measure episodic (Bonnici et al., 2016; Richter et al., 2016) and semantic memory (Davey et al., 2015). Together this emerging evidence is inconsistent with a role of the DMN in primarily off-task states, and instead, supports the hypothesis that this system, perhaps in combination with regions of the medial temporal lobe, may help determine the level of subjective detail in ongoing experience.

We also found that individuals who were more on-task had greater cortical thickness in an adjacent anterior region of parahippocampus. This region has relatively higher levels of connectivity with task-positive systems, in particular, the ventral attention network, and regions of right dorso-lateral prefrontal cortex that fall within the fronto-parietal system. Importantly, decoding the most likely functional associations of this region tended to reveal task-positive terms, providing evidence of a consistent conceptual mapping from patterns of self-reports of being on-task in the laboratory to the results of a formal meta-analysis of neuroimaging data. It is important to note, however, that the relationship between off-task states and so-called task-positive systems is likely to be complicated. For example, certain studies have found that task-positive systems such as the ventral attention network may help inhibit off-task thought. For example, Hasenkamp and colleagues (2012) found that in a sample of meditators, activity within the ventral attention network increased when individuals redirected their attention away from off-task information and back towards the task in hand. In contrast, other studies have suggested that task-positive systems can be important in off-task states. For example, Christoff and colleagues (2009) identified regions of the ventral attention as important during periods when attention was off-task, while Mason and colleagues (Mason et al., 2007) found that activity within the insula during well practiced tasks, was correlated with trait levels of daydreaming. Finally, Bernhardt and colleagues (2014) identified that regions of anterior cingulate cortex were thicker for individuals who reported more off-task thought in non-demanding situations. It is possible that such heterogeneous evidence reflects the possibility that certain domain general control systems provide support for cognition regardless of whether it is related to a goal in the environment or a personal goal in imagination (Christoff et al., 2016; Smallwood, 2013). Consistent with this view, a prior analysis of the resting state data included in this paper by Turnbull and colleagues (2019) demonstrated connectivity between the ventral attention network and a region of motor cortex was associated with greater level of off-task thought in the 0-back condition, and greater level of on-task thought during the 1-back condition.

In this context, it may be important that we have found individual variations in off-task thought was linked to differences in the relative strength of coupling between the two parahippocampus regions with other regions of the cortex. Individuals with more task focus tended to show patterns of heightened intrinsic functional connectivity between the anterior medial temporal lobe region and right hemisphere regions at the intersection between the default mode and frontal parietal networks. In addition, they had stronger connectivity between the posterior regions of the parahippocampus complex and a region of ventrolateral prefrontal cortex at the intersection within the default mode and ventral attention network in the left hemisphere. One of our prior studies found that connectivity between both right dorsal parietal cortex and right inferior frontal sulcus was linked to patterns of deliberate off-task thought (Golchert et al., 2017) and studies have shown that deliberate aspects of off-task thoughts tend to be reduced when task demands increase (Seli et al., 2016). In our study, PCA indicated an association between on-task states with more deliberate experiences. Our study, therefore, leads to a novel hypothesis - that trade-offs in communication between the anterior and posterior parahippocampus with different cortical regions could be important in distinguishing situations when cognition is focused on information pertinent to an external task or information self-generated based on internal representations.

Collectively, therefore, our findings place constraints on how the DMN, and in particular the medial temporal lobe, contribute to ongoing thoughts. For example, the current data cannot be readily be accounted for by the assumption that the DMN is simply task-negative in nature, since arguably the most straightforward conclusion from our study is that this system is linked to patterns of detailed task focus. Moreover, our study suggests that simple mappings between the medial temporal lobe and specific aspects of experience may be unrealistic since we found adjacent regions of medial temporal lobe with a strong association with patterns of task-focused experience. Instead, our data suggest the medial temporal lobe is important for multiple aspects of ongoing thought and this complex role is reflected by the web of connections it forms with other cortical regions. Extrapolating from our data, the wide ranging connections the medial temporal lobe forms with the cortex may not only allow it to support how cortical representations are reinstated during imagination

(Horner et al., 2016), or, drive the dynamics of spontaneous thoughts (Christoff et al., 2016) - we hypothesise that how the medial temporal lobe interacts with task-positive cortical regions may also influence whether ongoing thought is tethered to processes relevant to external goals or to self-generated patterns of experience.

A broader role of the medial temporal lobe in ongoing thoughts is consistent with contemporary accounts of this structure's neurocognitive function. The complex pattern of connectivity we have found to be associated with adjacent regions of the medial temporal lobe is consistent with component process accounts of the hippocampus which argue that the importance of this brain system emerges from its role in the flexible organisation of neural processing across the cortex (e.g. Moscovitch et al., 2016). More generally, our study suggests aspects of these connectivity patterns may reflect different functional modes. Computational accounts assume the ability for the medial temporal lobe to function in contrasting ways (such as playing a role in both encoding and retrieval) may emerge from the organising influence of temporal features of the theta rhythm (e.g. Hasselmo and Stern, 2014). Together, these mechanistic accounts of the medial temporal lobe provide a framework that not only can account for our findings, but also suggest a role for these systems that extends beyond memory retrieval to include acts of conceptual generalization (Constantinescu et al., 2016), real and imagined navigation (Horner et al., 2016) and simulations of the future (Buckner and Carroll, 2007; Schacter et al., 2007). Moreover, recent studies have shown that the so-called grid cells within the hippocampus, which are thought to be important for spatial navigation, are also sensitive to reward processing (Boccara et al., 2019; Butler et al., 2019). These results suggest that medial temporal lobe function extends beyond spatial processing. It is possible that part of this broad functional role may emerge because of a gradient along the long axis of the medial temporal lobe that differentially supports interactions with regions at the front and back of the cortex, with anterior regions linked with more abstract functions than those towards the back (de Wael et al., 2018). Aspects of this topographical gradient may be partly reflected in our results, in particular, the role of the anterior aspect of the medial temporal lobe may be important in maintaining processes relevant to specific tasks. It is also notable that many features of our analyses map closely onto the PMAT account of hippocampal – cortical functional interactions (Libby et al., 2012; Ritchey et al., 2015). This framework proposes that the parahippocampus has a closer functional alignment with DMN structures than do more anterior regions of the medial temporal lobe. Our study supports this view since we found that the more posterior region identified through our analysis of cortical thickness was more correlated with regions of the DMN than was the more anterior region. It is an interesting possibility for future work to consider how the PMAT framework can help establish the underlying neural processes that contribute to different patterns of ongoing thought.

Although our study provides further evidence that functions of the DMN play an important role in aspects of ongoing thought that extends beyond a simple task-negative account, it also leaves many important questions unanswered. For example, our analysis identified brain regions that are allied to unimodal cortex were linked to the modality of patterns of ongoing thought (i.e. whether it took the form of images or words). These data emphasise the contribution of more specialised region of the cortex to the form of representations that dominate experiences and so are broadly consistent with contemporary accounts of cognition. For example, the hub and spoke account of semantic processing (Patterson et al., 2007; Ralph et al., 2017) emphasises the role of modality specific cortex important for seeing, hearing and acting, in elements of semantic meaning. Similar accounts are offered for aspects of how the hippocampus retrieves episodic memories (Moscovitch et al., 2016). Our data may, therefore, illustrate the role that unimodal cortex plays in contributing to the form of experience, possibly through a process of step-wise integration from unimodal to transmodal regions within the DMN (Margulies et al., 2016) and that is perturbed in autism (Hong et al., 2019). However, our current study used a visual working memory paradigm that is suboptimal for distinguishing different modalities of experience. To do this more precisely, it would be important to sample ongoing thoughts in tasks that depend on different modalities (e.g. auditory and visual). Consequently, the modality aspect of our findings should be treated with caution until studies have examined these features of ongoing thought using experimental paradigms that are more suited to this question. More generally, the analyses performed in this study were based on evaluating processes important in ongoing thought (a state) through the lens of individual differences in both experiences and neural functions (a trait). An individual difference approach provides a powerful way to examine the processes underlying cognition in general, for example by offering the chance to test neurocognitive hypotheses with relatively large sample sizes (Yarkoni et al., 2011). However, it must be borne in mind that there are certain limitations to the conclusions drawn from this method. For example, there are likely to be important aspects of ongoing thoughts that can only be addressed through the simultaneous measurement of neural functions with measures of experience. In this regard it is important to note that associations between DMN processing and patterns of detailed thought were observed in our prior online experience sampling study (Sormaz et al., 2018). This provides confidence in the generalizability of this aspect of our findings. In the future, it will be important to use online experience sampling in conjunction with the tools of neuroimaging to understand how individuals maintain patterns of task-relevant thought across different situations, as this could allow insight into the possible roles of the anterior region of parahippocampus. It is also important to note that we currently have no a priori understanding of the dimensions that underpin patterns of ongoing experience. In the current work, similar to several of our prior studies (Ruby et al., 2013ab; Engert et al., 2014; Konishi et al., 2017; Karapanagiotidis et al., 2017; Medea et al., 2017; Smallwood et al., 2016; Sormaz et al., 2018; Turnbull et al., 2019), we focused on latent dimensions that emerge when experience is measured using a wide range of questions. This approach has been successfully validated through associations with metrics from both brain, behaviour and physiology, however, it is possible that by focusing on latent variables, our dimensional approach may obscure relationships that can be determined with a more targeted analysis. Furthermore, it seems likely that important dimensional properties of experience may be overlooked in our study because the set of questions we used may have missed important aspects of experience. Accordingly, the most important inference that should be derived from our study is that accounts of the DMN which focus on contribution to patterns of off-task autobiographical information rather than a role in subjective detail, are insufficient for describing the role this system plays in human cognition. Finally, as our study shows links between cortical thickness and patterns of ongoing thought, it raises the possibility that variables such as smoking, alcohol use or medication that can contribute to changes in brain structure (e.g. Durazzo et al., 2011; Kühn et al., 2010; Nesvåg et al., 2008) may also influence experience. Studies have found that both alcohol and smoking influence momentary changes in experience (Sayette et al., 2009; Sayette et al., 2010) and future work could investigate the possibility that these variables are reflected in the structure of experience at longer time frames.

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