

RESEARCH ARTICLE

Hello, is that me you are looking for? A re-examination of the role of the DMN in social and self relevant aspects of off-task thought

Charlotte Murphy^{1*}, Giulia Poerio², Mladen Sormaz¹, Hao-Ting Wang¹, Deniz Vatansever¹, Micah Allen³, Daniel S. Margulies⁴, Elizabeth Jefferies¹, Jonathan Smallwood¹

1 Department of Psychology, University of York, York England, United Kingdom, **2** Department of Psychology, The University of Sheffield, Sheffield, England, United Kingdom, **3** Cambridge Psychiatry, Cambridge University, Cambridge, United Kingdom, **4** FRONTLAB, ICM—Hôpital Pitié Salpêtrière, Paris, France

* charlotte.murphy@york.ac.uk.



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Citation: Murphy C, Poerio G, Sormaz M, Wang H-T, Vatansever D, Allen M, et al. (2019) Hello, is that me you are looking for? A re-examination of the role of the DMN in social and self relevant aspects of off-task thought. PLoS ONE 14(11): e0216182. <https://doi.org/10.1371/journal.pone.0216182>

Editor: Tyler Davis, Texas Tech University, UNITED STATES

Received: April 11, 2019

Accepted: October 15, 2019

Published: November 7, 2019

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Data Availability Statement: All files produced in these analyses are freely available at Neurosynth at the following URL: <http://neurovault.org/collections/2364/>.

Funding: This study was supported by awards to JS from the ERC (WANDERINGMINDS - 646927), the Volkswagen Foundation (Wandering Minds - 89440 and 89439) and the John Templeton Foundation, “Prospective Psychology Stage 2: A Research Competition”. EJ was supported by grant FLEXSEM-771863 from the ERC.

Abstract

Neural activity within the default mode network (DMN) is widely assumed to relate to processing during off-task states, however it remains unclear whether this association emerges from a shared role in self or social content that is common in these conditions. In the current study, we examine the possibility that the role of the DMN in ongoing thought emerges from contributions to specific features of off-task experience such as self-relevant or social content. A group of participants described their experiences while performing a laboratory task over a period of days. In a different session, neural activity was measured while participants performed Self/Other judgements (e.g., Does the word ‘Honest’ apply to you (Self condition) or Barack Obama (Other condition)). Despite the prominence of social and personal content in off-task reports, there was no association with neural activity during off-task trait adjective judgements. Instead, during both Self and Other judgements we found recruitment of caudal posterior cingulate cortex—a core DMN hub—was above baseline for individuals whose laboratory experiences were characterised as detailed. These data provide little support for a role of the DMN in self or other content in the off-task state and instead suggest a role in how on-going thought is represented.

Introduction

The human mind is not always occupied by our actions in the moment: everyday experience is replete with thoughts that are generated based on representations from memory, rather than events in the here and now [1]. Since the turn of the century, an increasing experimental focus on states of self-generated thought, often under the rubric of mind-wandering [2] has revealed links with health, well-being and productivity [3]. This research endeavour has been enhanced and supported by the discovery of the default mode network (DMN), a distributed set of regions spanning medial and lateral, frontal, parietal and temporal cortices [4]. Unlike other

Competing interests: The authors have declared that no competing interests exist.

neural systems, the DMN regions deactivate during effortful external processing [4], and these so-called “task-induced deactivations” were highlighted as a potential analogue to the processes occurring during off-task cognitive states [5].

Subsequent research broadly corroborated this idea. Studies combining experience sampling with measures from neuroimaging demonstrated increased activity in the DMN during off-task states [6, 7]. While others found tasks which mimic the content that people report during the off-task state, such as mental time travel and self-relevant or social cognition, modulate the DMN (for a review see [3, 8]). Although these studies provide evidence of associations between the DMN and off-task thought, the broader view of this system as task-negative has been challenged [9]. For example, recent studies of connectivity during cognitive tasks have shown that the DMN communicates selectively with task positive systems [10], and that DMN activity can increase during cognitive task that require internally represented information or task rules [11, 12, 13, 14]. If the functions of the DMN are not task-negative *per se* then this would undermine a simple one-to-one mapping of DMN activity and content processed in the off-task state.

An alternative perspective on the functional role of DMN in cognition emerges from a consideration of its status within the broader cortical landscape [15]. In humans and other primates, regions of the DMN are located at points on the cortex that are maximally distant from regions of unimodal cortex, in both functional and structural space [16]. Increased topographical distance from unimodal systems may help segregate neural signals in the DMN from sensory input, explaining why neural activity within this network has a unique relationship to task behaviour (i.e. task-induced deactivations). The cortical organisation giving rise to functional isolation is thought to represent a hierarchy which supports the progressive integration of information from unimodal regions to transmodal regions, the most extreme of which are in the DMN, supporting increasingly abstract neural representations [17]. In this view, the DMN reflects a set of closely allied hubs that form an integrative cortical backbone vital for the maintenance of cortical dynamics [15]. If the DMN reflects a collection of integrative hubs, then it is likely to be linked to broadly distributed patterns of cortical activity that may determine relatively global features of ongoing cognition, rather than specific aspects of mental content.

In a prior study [18], we re-evaluated the relationship between neural activity and momentary patterns of ongoing thought, taking advantage of both recent advances in experience sampling—that describe dimensions underlying multiple aspects of self-reported experience—and imaging analysis methods. Neural function was recorded using functional magnetic resonance imaging (fMRI) while participants alternated between blocks of a 0-back and 1-back working memory task. During working memory maintenance (i.e. the 1-back condition), representational similarity analysis indicated that patterns of activity within the DMN were associated with the level of subjective detail in experience reported by participants. This aspect of detailed cognition, did not load strongly on task focus (i.e., how on task the participant was), but was elevated during the harder 1-back task, suggesting that it represent levels of active detail regarding the task. Importantly, therefore, patterns of activity within the DMN was linked to variation in relative levels of detail in experience during the harder task and so contributed to participant’s experiences when they were more engaged with an external task. Critically, regions in the DMN did not contain information regarding the off-task state, although this aspect of experience could be predicted in regions of sensory motor cortex. This pattern of results, therefore, challenges notions of the DMN as either being necessary or sufficient for the engagement of task irrelevant cognition since (a) the level of subjective detail could be predicted by patterns within the DMN during an active task state and (b) whether attention was focused on the task could be predicted by neural signals in regions other than the DMN.

An alternative to the task negative view is the possibility that the role of the DMN in ongoing thought emerges from contributions to specific features of off-task experiences, such as self-relevant or social content [7, 19, 20]. For example, individuals who spend a lot of time engaged in off-task thoughts about themselves or other individuals may have DMN that are highly responsive to information of this nature. This *hyper-responsivity* hypothesis gains support from studies, from different geographic populations, showing off-task thoughts often have high-levels of self-relevant content [3]. These include in Australia [8], Belgium [7], China [21], Germany [22], the UK [23], and the US [24]. This hypothesis is hard to test in our prior study [18] since neural activity was sampled in a working memory paradigm, when the content of ongoing cognition is most dissimilar to those that emerge in the off-task state [25]. Therefore, any relationship that was related to particular aspects of content (such as its self-relevance) could have been obscured in our prior study because the visuo-spatial memory task lacked meaningful semantic or personally applicable content. It remains a possibility that individuals who report high levels of off-task thought with self-relevant or social content in the context of a semantically impoverished laboratory task, do so because their DMNs show high levels of responsiveness to processing these categories of information.

To test this possibility, the current study examined whether greater levels of responsiveness to personally relevant or socially relevant content in the DMN was related to greater levels of off-task thoughts with similar content in the laboratory. In the current study we measured whole-brain activity while participants make trait judgements about themselves and a significant other. This manipulation has been shown to modulate activity within the DMN [26], and can lead to increases in off-task thoughts in the lab (e.g. [27]). On a separate series of behavioural sessions, we measured patterns of thought in the laboratory in the same individuals. Notably, if DMN activity during off-task states reflects hyper-responsivity to content that is common in that state, then the expression of self-relevant or social off-task mental content in the laboratory, could be linked to greater recruitment of this network while making personal or social judgements during trait adjective judgements. In contrast, if the DMN is important for broader aspects of ongoing experience, rather than just its contents, then neural activity within this system could show a positive correlation with descriptions of more abstract features of ongoing thought in the laboratory (i.e. its detail).

Methods

Participants

In total, structural and resting-state scans were collected in one MRI session for 207 participants (females = 132, $M_{\text{age}} = 20.2$, $SD = 2.35$ years). All 207 participants also took part in a multidimensional experience sampling (MDES) study across three separate laboratory sessions. All laboratory sessions were scheduled within a week of the initial MRI session. In addition, 65 participants out of the original 207 agreed to return for a self-reference fMRI experiment that took place in a second MRI session (41 females; $M_{\text{age}} = 21.4$, $SD = 2.67$). The study received ethical approval from the York Neuroimaging Centre and the University of York Psychology Department. All investigation was conducted according to the principles expressed in the Declaration of Helsinki and participants provided written informed consent.

Multidimensional experience sampling (MDES)

In the laboratory we used a block design to assess the contents of experience during a simple working n-back task (0-back; 1-back) (for prior published examples of this task see [18, 28, 29]) across three separate sessions. Participants completed target and non-target trials. In non-target trials, a pair of shapes appeared on screen. The pairs consisted of a circle and a square, a

circle and a triangle, and a square and a triangle, each in two different left/right configurations for a total of six possible pairs. Following an unpredictable sequence of non-target trials, a target trial was presented in which participants had to make a manual response to a small stimulus presented in the centre of the screen in either blue or red across conditions, with the colour counterbalanced across participants. In the 0-back condition, the target was flanked by one of two shapes, and participants had to indicate which shape matched the target shape by pressing the appropriate button. In the 1-back condition, the target was flanked by two question marks, and participants had to respond depending on which side the target shape had been on during the prior trial. Presentation times for fixation crosses ranged from 1.3 to 1.7 s in steps of 0.05 s, and non-target presentation times varied from 0.8 to 1.2 s in steps of 0.05 s. Target presentation times always ranged from 2.1 to 2.5 s in steps of 0.05 s, and a response from participants did not end the target presentation. There were 8 blocks in one session and each block consisted of two to four mini-blocks. Each block contained either the 0-back or the 1-back condition. Each mini-block consisted of one target trial and a varied number of non-target trials preceding the target trial (between one and six non-target trials). Conditions were counterbalanced across participants. In total, the eight blocks lasted around 25 min. This task protocol is summarised in Fig 1.

In order to sample different features of participants' ongoing experiences during the n-back task, we used multidimensional experience samples (MDES; [19]). This technique uses self-report data to assess the contents of experience on a number of dimensions. Participants answered 13 questions (see Table 1) on a 4-point scale ranging from 0–1. The first thought probe asked participants to rate their level of task focus (“My thoughts were focused on the task I was performing”) on a sliding scale from 0 (completely off-task) to 1 (completely on task). Participants then answered 12 randomly presented questions regarding the content and form of their experience in the moments just before they answered the first thought probe (on level of task focus). MDES probes occurred on a quasi-random basis to minimise the likelihood of anticipating the probes. At the moment of target presentation there was a 20% chance of a MDES thought probe being presented instead of a target, with a maximum of one probe per block of the 0-back/1-back task. In each of the three sessions, an average of 14.07 (SD = 3.30, range = 6–25) MDES probes occurred; in the 0-back condition, an average of 7.02 (SD = 2.36, range = 2–14) MDES probes occurred; and in the 1-back condition, an average of 7.04 (SD = 2.24, range = 1–15) occurred (average of 42 probes per participant across all three sessions).

Resting-state fMRI

Procedure. All 207 subjects completed a 9-minute resting-state MRI scan during which they were asked to rest in the scanner with their eyes open.

Resting-state fMRI acquisition. Structural and functional data were acquired using a 3T GE HDx Excite MRI scanner with an 8-channel phased array head coil (GE) tuned to 127.4 MHz, at the York Neuroimaging Centre. A gradient-echo EPI sequence was used to collect data from 60 axial slices with an interleaved (bottom-up) acquisition order with the following parameters: TR = 3 s, TE = minimum full, volumes = 180, flip angle = 90°, matrix size = 64 × 64, FOV = 192 × 192 mm, voxel size = 3 × 3 × 3 mm. A minimum full TE is the shortest TE the scanner would permit for the scanning parameters used (on average ~ 18ms). This was selected to optimise image quality (as opposed to selecting a value less than minimum full which, for instance, would be beneficial for obtaining more slices per TR). Functional images were co-registered onto a T1-weighted anatomical image from each participant (TR = 7.8 s, TE = 3 ms,

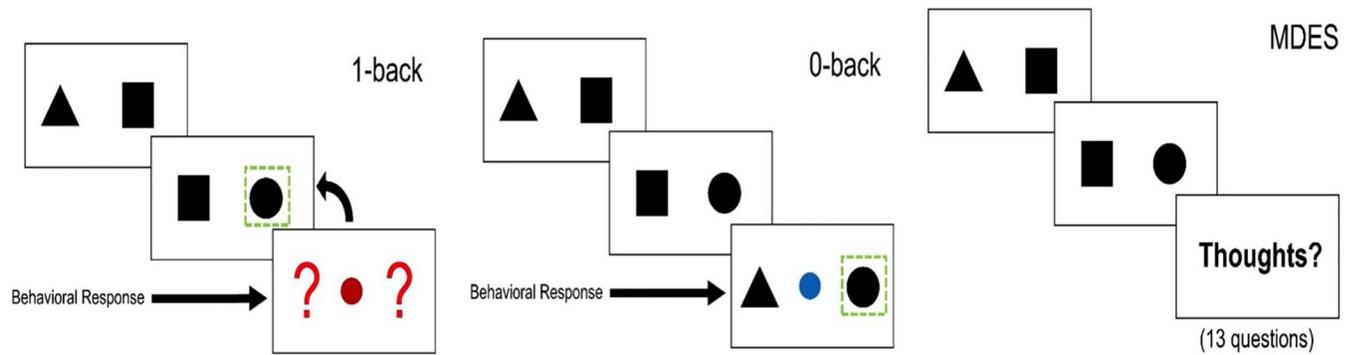


Fig 1. Multidimensional Experience Sampling (MDES). An n-back task was used to measure on-going thought in the laboratory, which alternated between an easy 0-back task and a more demanding 1-back task. In non-target trials, a pair of shapes appeared on screen. Following an unpredictable sequence of non-target trials, a target trial was presented in which participants had to make a manual response. Left-hand panel: in the 1-back condition, the target was flanked by two question marks, and participants had to respond depending on which side the target shape had been on during the prior trial. Middle panel: in the 0-back condition, the target was flanked by one of two shapes, and participants had to indicate which shape matched the target shape by pressing the appropriate button. Right-hand panel: at the moment of target presentation there was a 20% chance of a MDES thought probe being presented instead of a target. Participants answered 13 questions (see Table 1) on a 4-point scale ranging from 0–1. The first thought probe asked participants to rate their level of task focus (“My thoughts were focused on the task I was performing”) on a sliding scale from 0 (completely off-task) to 1 (completely on task). Participants then answered 12 randomly presented questions regarding the content and form of their experience in the moments just before they answered the first thought probe (on level of task focus).

<https://doi.org/10.1371/journal.pone.0216182.g001>

FOV = 290 mm x 290 mm, matrix size = 256 mm x 256 mm, voxel size = 1 mm x 1 mm x 1 mm).

Self-reference fMRI task (n = 65)

Procedure. In the scanner, participants completed a trait-adjective judgement paradigm where participants had to associate certain traits to themselves (‘Self’) or another person (‘Other’). Trials began with a 9 second fixation cross, followed by a 6 second presentation of a neutral valence adjective taken from a set of norms [30]. Participants decided whether the word applied to them (Self) or Barack Obama (Other). For instance, does ‘honest’ apply to Barack Obama? Responses (yes/no) were made after the six-second contemplating period using a button response. Participants had three seconds to make their decision. In both conditions 15 trials occurred and words were fully counterbalanced.

Table 1. Multi-Dimensional experience sampling questions used this experiment.

Dimensions	Questions	0	1
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
Detail	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
Spontaneous	My thoughts were:	Spontaneous	Deliberate

<https://doi.org/10.1371/journal.pone.0216182.t001>

MRI acquisition. Structural and functional data were acquired using a 3T GE HDx Excite MRI scanner with an 8-channel phased array head coil (GE) tuned to 127.4 MHz, at the York Neuroimaging Centre. Structural MRI acquisition was based on a T1-weighted 3D fast spoiled gradient echo sequence (TR = 7.8 s, TE = min full, flip angle = 20°, matrix size = 256 x 256, 176 slices, voxel size = 1.13 x 1.13 x 1 mm). Functional data was recorded 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 mm³, 180 volumes). A FLAIR scan with the same orientation as the functional scans was collected to improve co-registration between scans.

Data analysis

Principal component analysis (PCA) of MDES data. We created a single 8694-by-13 matrix in which each row was a MDES probe (8694 = 207 participants x 42 probes) and each column was a question. We used PCA with varimax rotation in SPSS version 24 to reduce the dimensionality of these data using scree plots to determine that 4 principal components should be extracted (see S1 and S2 Figs). The resulting data were used as regressors of interest at the participant level in the self-reference experiment. The component names were decided by naming each after the highest loading item if the component was anchored at one end (e.g. Detail). If they were anchored by opposing scores (e.g., Words and Images) we named them based on the distinction that these loadings imply (e.g. Modality).

Self-reference task analysis. For the analysis of neural activity during the self-reference task, functional and structural data were pre-processed and analysed using FMRIB's Software Library (FSL version 5.0, <http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FEAT/>). Individual FLAIR and T1 weighted structural brain images were extracted using BET (Brain Extraction Tool). Structural images were registered to the MNI-152 template using FMRIB's Linear Image Registration Tool (FLIRT). The functional data were pre-processed and analysed using the FMRI Expert Analysis Tool (FEAT). Individual subject analysis involved: motion correction using MCFLIRT; slice-timing correction using Fourier space time-series phase-shifting; spatial smoothing using a Gaussian kernel of FWHM 6mm; grand-mean intensity normalisation of the entire 4D dataset by a single multiplicative factor; highpass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma = 100 s); Gaussian lowpass temporal filtering, with sigma = 2.8s.

First level analyses modelled the two experimental conditions (Self and Other). For each condition, these were modelled as six-second boxcar regressors modelling the entire presentation of the trait adjective (e.g., 'honest'), during which participants had to think about whether that trait applied to them (Self condition) or Barack Obama (Other condition). The response to each condition was contrasted against rest. Boxcar regressors for each condition in the general linear model were convolved with a double gamma hemodynamic response function (FEAT, FSL). Nuisance regressors that model motion parameters were also included as confound EVs in the model to account for head motion. First level effects were entered into a group analysis using a mixed-effects design (FLAME, <http://www.fmrib.ox.ac.uk/fsl>). Z-stat maps were generated for each EV; Self and Other. These maps were then registered to a high resolution T1-anatomical image and then onto the standard MNI brain (ICBM152).

We performed two group-level analyses on the task data using FLAME. To identify the spatial distribution of the regions modulated by the nature of the referent during trait adjective assessment, we compared Self > Other and Other > Self. Both spatial maps are thresholded at Z = 3.1 and are controlled for multiple comparisons (p < .05, FWE). In addition we calculated the effect of task (Self and Other judgements) > rest (S3 Fig). To understand the relationship between neural processing during each referent and experience in the laboratory, we

performed group-level regressions in which the spatial maps for each task, relative to baseline, where the dependent variables and the mean loadings for each individual for each MDES component were included as between participant continuous explanatory variables.

Resting state fMRI analyses. Resting-state data pre-processing and statistical analyses were carried out using the SPM software package (Version 12.0), based on the MATLAB platform (Version 15a). For pre-processing, functional volumes were slice-time and motion-corrected, co-registered to the high-resolution structural image, spatially normalised to the Montreal Neurological Institute (MNI) space using the unified-segmentation algorithm [31], and smoothed with an 8 mm FWHM Gaussian kernel. With the goal of ensuring that motion and other artefacts did not confound our data, we first employed an extensive motion-correction procedure and denoising steps, comparable to those reported in the literature [32]. In addition to the removal of six realignment parameters and their first-order derivatives using the general linear model (GLM) [33], a linear de-trending term was applied as well as the CompCor method that removed five principle components of the signal from white matter and cerebrospinal fluid [34]. Moreover, the volumes affected by motion were identified and scrubbed based on the conservative settings of motion greater than 0.5 mm and global signal changes larger than $z = 3$. Out of the 207 participants, a total of fifteen participants, who had more than 15% of their data affected by motion was excluded from the analysis [35]. Therefore, all resting-state analyses reported are based on a sample size of 192 participants. Finally, a band-pass filter between 0.009 Hz and 0.08 Hz was employed in order to focus on low frequency fluctuations.

Following this procedure, two seed regions were generated from the univariate maps of Self > Other and Other > Self regressed against our detail PCA (see Fig 2). This yielded two clusters centred on caudal posterior cingulate cortex for Self > Other [MNI: -2, -58, 26] and intracalcarine cortex for Other > Self [MNI 16, -84, 4]. We used the entire cluster identified in Fig 2 for this seed-based analysis (see S2 Table). The Conn functional connectivity toolbox (Version 15.h) [36] was used to perform seed-based functional connectivity analyses for each subject using the average signal from the spheres placed on the MNI coordinates for the two regions of interest (ROIs) described above. All reported clusters were corrected for multiple comparisons using the Family-Wise Error (FWE) detection technique at the .05 level of significance (uncorrected at the voxel-level, .001 level of significance).

Results

We applied PCA to the trial level data produced by MDES. This method describes the underlying dimensions within the patterns of responses in the experience sampling data. These can be broadly understood to be ‘patterns of thought’ captured in our study. Based on the scree plot (see S1 Fig), we identified four components that described 54.94% of the variance in our data and the loading of each item in each dimension are presented in the form of word clouds in the grey box in Fig 2. Component 1 described high loadings on detailed and evolving thoughts (Detail). This corresponds to the pattern of experience linked to the DMN in our prior study [18]. Component 2 described low loadings on the task and deliberate thought and higher loadings on self, future and person thoughts (Task). This component corresponds to the off-task state since it places personal and socially relevant content in opposition to a deliberate focus on the task. Component 3 described positive loadings on images and negative loadings on words and so corresponded to variation in the modality of experience (Modality). Component 4 describes high loadings on positive affect (Emotion). Note that these patterns are derived from the application of MDES to the larger sample of 207 individuals as this provides the most stable estimation of these dimensions. We repeated this analysis pipeline on the subset of

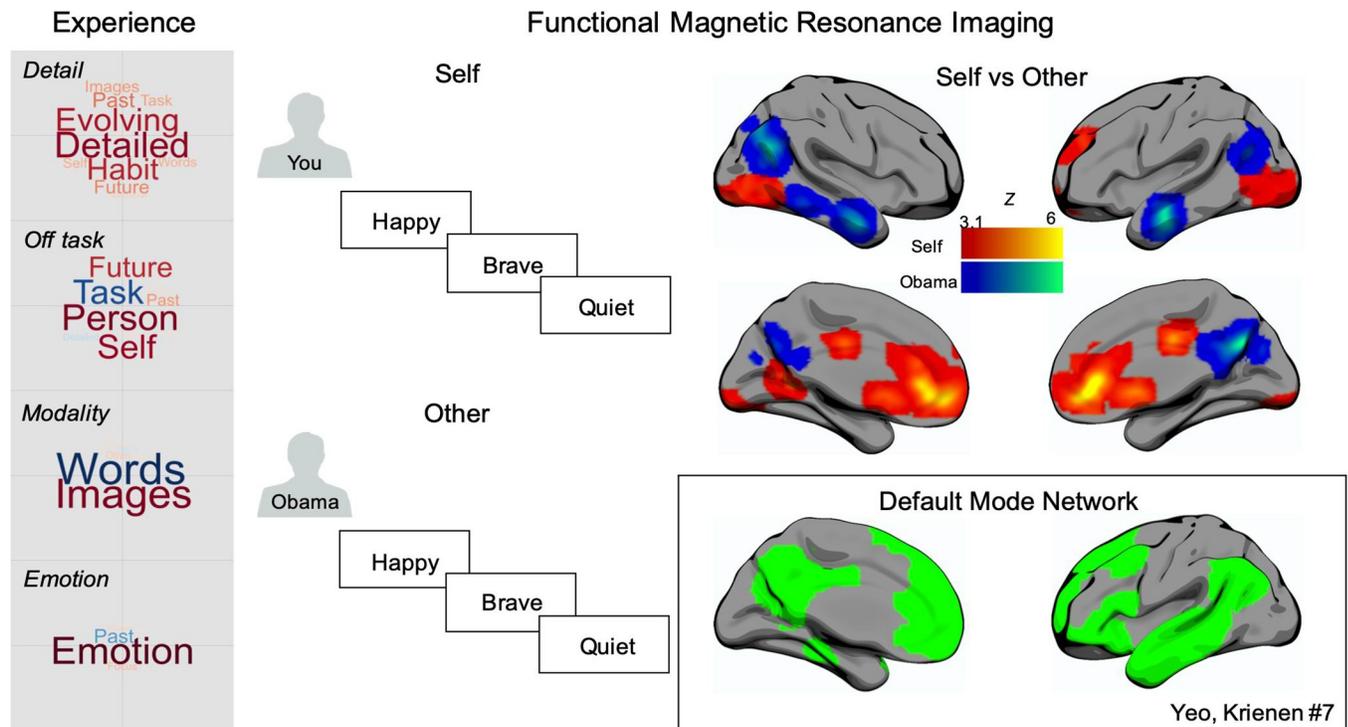


Fig 2. Patterns of thought during the laboratory and the modulation of neural activity during the self-reference task. The panel on the left-hand side displays the components of thought determined by the application of Principal Components Analysis to the Multi-Dimensional Experience Sampling (MDES) using a sample of 207 individuals. The size of the word describes the strength of the loading and the colour identifies whether the loadings is positive (warm) or negative (cool). The central panel describes the block design used to assess neural processing during a self-reference task in the scanner. The brains display the spatial distribution of the regions identified through a contrast of activity between Self and Other referent conditions. Warm colours highlight regions showing more activity during Self judgements compared to Others, and cool colours show regions showing more activity in Other (Obama) judgements compared to Self. The spatial maps are thresholded at $Z = 3.1$ and are controlled for multiple comparisons ($p < .05$, FWE). The box in the lower right hand corner shows the DMN as defined in the 7-network solution [37].

<https://doi.org/10.1371/journal.pone.0216182.g002>

individuals who also performed the self-reference task, yielding very similar scree plot (see [S1 Fig](#)) and pattern of loadings (see [S2 Fig](#)). In addition, in our prior study we demonstrated that the patterns derived using PCA describing each loading, generalised to different data collected in the same individuals. In particular, the pattern of loadings seen when participants performed the task in the scanner were similar to those identified in the lab (i.e. the item loadings for components were positively correlated) and patterns of both detailed thought and off-task thought showed positive correlations across individuals (i.e. individuals who were high on one dimension in the scanner were also high on the same dimension in the lab (see [18] for further details).

The comparison of differential neural activity when participants made self-reference judgements in the scanner is presented in the right hand panel of [Fig 2](#) ([S1 Table](#)). Manipulation of the referent (Self or Other) upon which trait judgements were made successfully modulates activity within the DMN. When making decisions about the Self compared to Other, activity was higher in regions of ventromedial prefrontal cortex, as well as in two regions of posterior cingulate cortex. When relating adjectives to Barack Obama compared to Self, activity was higher in regions of angular gyrus, lateral temporal cortex, as well as in the core of the posterior cingulate. All the regions modulated by the referent of the trait-adjective judgement, with the exception of ventral lateral occipital activity, fall within the DMN as defined by [37] (see inset to [Fig 2](#)). The modulation of activity within the DMN by different traits is broadly consistent

with the general importance for the temporal lobe regions in social cognition and from prior studies similar to this one [3]. Likewise meta-analyses suggest greater involvement of frontal DMN regions during self-relevant processing [38].

Next, we considered how patterns of experience in the lab are related to the neural activity during the self-reference task. We performed separate group-level regressions in which the dependent variables were maps of neural activity from each condition (Self and Other) contrasted against baseline. Each individual's average score on each MDES component from the laboratory was included as between individual explanatory variables. This analysis identified neural regions in both task conditions that increased activity from baseline levels, in proportion to how detailed an individual's thought was in the lab. These are presented in Fig 3 (S2 Table). In the Other condition, participants whose thoughts were more detailed had greater activity in a region of medial occipital cortex. This is presented in cool colours. In addition, during the Self condition, recruitment of caudal posterior cingulate cortex (PCC)—a core hub of the DMN—was greater for participants whose laboratory experiences were characterised as detailed and evolving. This is presented in warm colours in Fig 3. Scatter plots describing both effects are presented in the left-hand lower panel.

Notably, the PCC region of the DMN that showed greater activity during self-reference for participants who tended to have detailed and evolving experiences in the lab (Fig 3), also tended to show generally stronger activation when rating adjectives of another (Obama) rather than the Self (see Fig 1 and the results of a formal conjunction analysis in S5 Fig). This indicates that the region that shows an association with detail in the lab during self-reference tends to have higher activity when considering whether adjectives applied to Obama. To visualise the relationship between these two spatially overlapping effects, we plotted the signal change in this region of caudal posterior cingulate cortex in both conditions, separating individuals into those who were above (High) and below (Low) the median for detail thinking in the lab (see lower right-hand panel in Fig 4). Please note that the median split are utilised for visualisation purposes only.

In contrast to the effects of detail there were no regions in a whole-brain analysis significantly associated with the extent of off-task thinking in the lab, and post-hoc analysis indicated no association between neural processing in either the posterior cingulate cortex, or the lingual gyrus (all r -values $< .15$, all p -values $> .6$). We also tested whether the contrast between Self and Other conditions was significantly related to variation in either dimension of experience as measured in the lab. This revealed no differences that were related to variation in either the levels of subjective detail or with off-task focus. This absence of an association between patterns of off-task content in the laboratory, and the level of responsiveness of DMN regions to social or other relevance judgements is inconsistent with a simple view of off-task thoughts as resulting from hyper responsiveness to these types of information in the DMN. However, while the method of whole-brain analysis used in our prior analysis is well suited to the identification of positive relationships between patterns of neural activity and ongoing thought, it is possible that it may obscure important sub-threshold relationships between off-task thinking and patterns of neural activity.

To rule out the possibility that our failure to find evidence of associations with off-task thinking is a Type 2 error we conducted an ROI analysis. To do this, we selected all of the regions that showed significant responses to the self-other judgements during the fMRI session (a total of 10 regions of interest) (see Table 2 and S1 Table). Using these ROIs we compared their signal change (relative to baseline) in both conditions of the experiment separately, to both patterns of detail and off-task thinking (a total of 40 comparisons).

This analysis revealed significant positive associations with detailed thinking in the posterior cingulate cortex in one region linked to social cognition (posterior cingulate cortex, $r =$

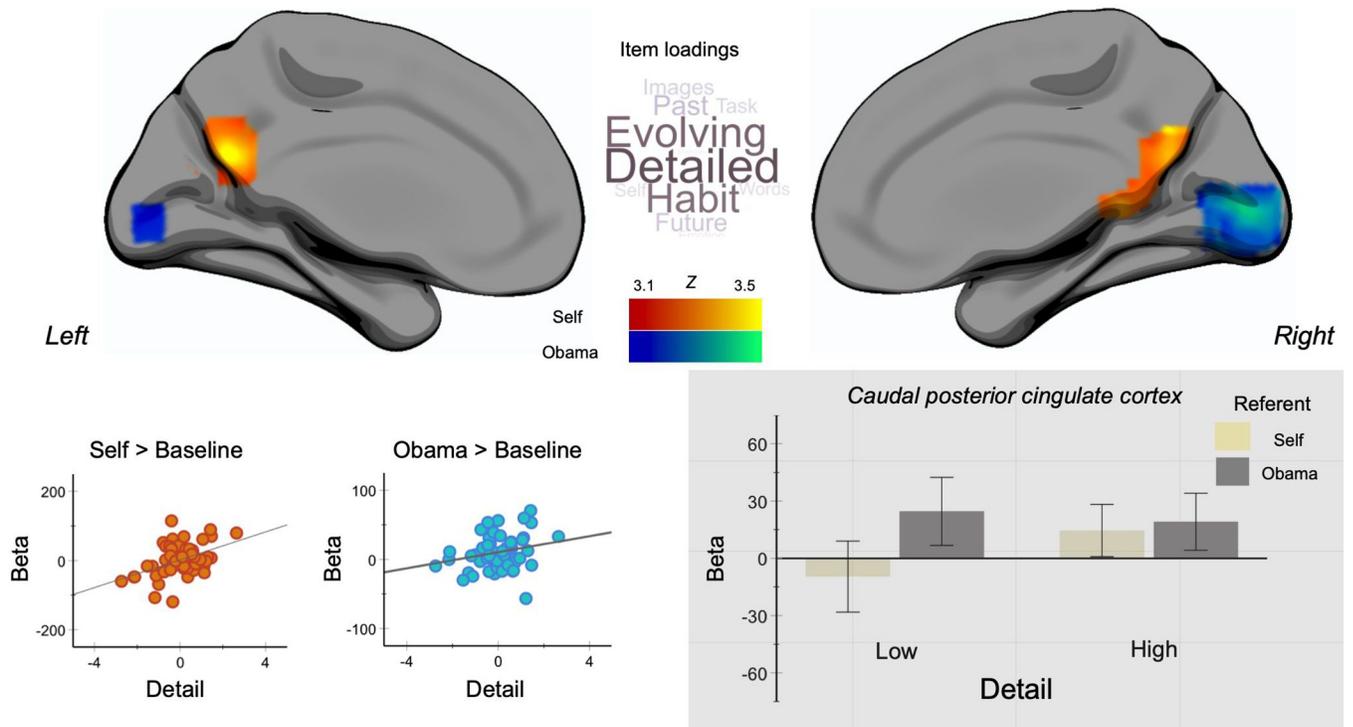


Fig 3. The relationship between patterns of ongoing thought in the laboratory and neural activity during trait adjective judgements. Warm colours describe regions whose neural activity during self-trait judgements was correlated with levels of detail in ongoing experience in the lab. Cool colours describe regions whose neural activity during other-trait judgements was correlated with the level of detail in ongoing thought. Spatial maps were thresholded at $Z = 3.1$ controlling for multiple comparisons $p < .05$ (FWE). The scatter plots display the association between individual's detail component score and neural activity extracted from posterior cingulate cortex (PCC) (warm colours) and medial occipital cortex (cool colours) respectively. Notably, the PCC cluster also showed a selective increase when making trait judgements regarding Barack Obama relative to the Self (see Figs 2 and S4). The bar graph in the grey inset shows the signal in the caudal PCC cluster in each condition (Self / Other) plotted for individuals whose thoughts in the lab were below (Low) and above (High) the median for the Detail dimension. Thus, individuals who engaged in detailed thought within the laboratory recruited caudal posterior cingulate cortex above baseline when making trait adjective judgements based on either Self or Other as the source of the judgement. The error bars indicate the 95% C.I. The word cloud summarises the pattern of loadings that correspond to the detail component. Larger fonts describe a higher loading.

<https://doi.org/10.1371/journal.pone.0216182.g003>

.31, $p < .05$, although left angular gyrus showed a trend towards significance, $r = .26$, $p = .051$. Greater detail was also associated with the lateral occipital cortex during self-relevance ($r = .31$, $p < .05$). Note that the pCC and LOC correlations are redundant with the whole-brain results reported earlier and they are only mentioned here for the sake of completeness. No regions showed a significant negative correlation between activity and the levels of detail. In contrast, a region of caudal posterior cingulate cortex showed a significant negative association between off-task thought and neural processing during self-relevance ($r = -.31$, $p < .05$). This region of the DMN was therefore less active during self judgements for individuals who tended to think about themselves frequently in the lab. Thus a more liberal ROI analysis found no support for the view that hyper responsiveness in regions of the DMN to personally or self-relevant content is linked to the expression of off-task thought in semantically impoverished conditions.

In order to quantify the strength of the evidence in favour of the null hypothesis we conducted a Bayesian analysis of the associations produced via our ROI analysis (for review of method see [39]). The Bayesian framework allows us to quantify how much more likely the data are under the null hypothesis compared to the alternative hypothesis. The Bayes inference about Pearson correlation coefficient measures was conducted in SPSS (version 25) using default settings. This analysis permits Bayesian inferences to be drawn by estimating Bayes

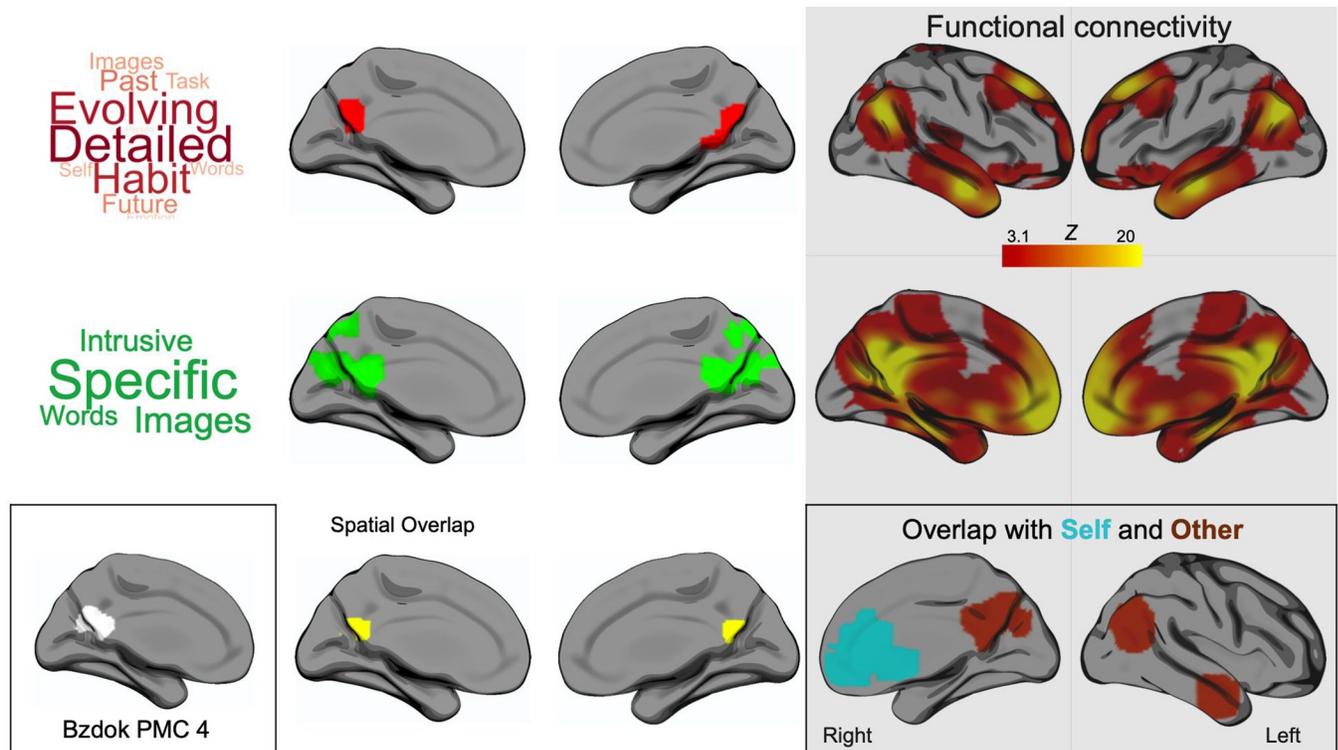


Fig 4. Converging evidence for a relationship between caudal posterior cingulate cortex and levels of specific detail in ongoing experience. (A) Top panel: shows the spatial distribution of areas associated with patterns of detailed thought in the lab and during self-reference in the scanner (red). Middle panel: shows the results of an individual difference analysis from our prior study [19] showing associations between medial temporal lobe connectivity and the posterior cingulate indicating more detailed thoughts (green). Bottom panel: These overlap in the area in yellow indicated in the lower panel. The inset on the bottom left shows a corresponding region of posterior cingulate cortex that was identified using decompositions based on both task and task-free data which was related to a combination of mental processes including language processing [41]. (B) Shows the functional connectivity of the overlap of both of the empirical studies, higher correlations are indicated in warmer colour. This pattern of connectivity captures the regions that show a pattern of modulation for both Self and Other referents during the self-reference task as can be seen in the yellow 'spatial overlap' cluster. The functional connectivity maps are corrected for multiple comparisons using the Family-Wise Error (FWE) detection technique at the .05 level of significance (uncorrected at the voxel-level, .001 level of significance). Note that the items in the word clouds differ due to the use of different self-report items in each of the experiments.

<https://doi.org/10.1371/journal.pone.0216182.g004>

factors; which can quantify the degree to which the data favour one of two hypotheses. To compute this we first selected all of the regions that showed significant responses to the self-other judgements during the fMRI session (a total of 10 regions of interest) (see Table 2 and S1 Table). Using these ROIs we compared their signal change (relative to baseline) in both conditions of the experiment separately, to both patterns of detail and off-task thinking (a total of 40 comparisons), and a Bayes factor for each pairwise comparison was computed (see Table 2). This revealed that the Bayes Factor in support of the null hypothesis was greater than 3, a pattern of moderate evidence for the null hypothesis, for 17 out of the 20 comparisons with off-task thought. Table 2 presented the distribution of r-values and Bayes factors for each of the correlations.

Finally, to examine the generalisability of the association found between neural processing in caudal posterior cortex and detailed thought in the laboratory we compared the current data to a similar region identified in a prior study [19]. This study analysed the resting-state connectivity of DMN nodes including those in the temporal lobe (the temporal pole and hippocampus) and their relationship to patterns of ongoing thought in the laboratory, using a similar laboratory paradigm to the one in the current experiment. Connectivity between a region of medial temporal lobe, and, a region of posterior cingulate cortex was stronger for

Table 2. Bayesian analysis results.

Contrast	Cluster	Brain Regions	MNI co-ordinates	# voxels	Self>Other		Other>Self	
					PCA1—Detail	PCA2 –OffTask	PCA1—Detail	PCA2—OffTask
Self > Other	1	Medial prefrontal cortex	0 40 0	2694	r = .21 BF = 2.81	r = -.14 BF = 5.63	r = -.05 BF = 9.01	r = -.05 BF = 9.03
	2	L. Precuneus/PCC	-22-52 6	1704	r = -.05 BF = 8.97	r = -.21 BF = 2.79	r = -.17 BF = 4.25	r = -.11 BF = 6.90
	3	R. Occipital fusiform gyrus	20-88-14	1002	r = -.11 BF = 7.10	r = -.21 BF = 2.72	r = -.16 BF = 4.73	r = -.10 BF = 7.43
	4	Anterior cingulate gyrus	-2-18 32	259	r = .20 BF = 3.36	r = -.32 BF = 0.55	r = .14 BF = 5.70	r = -.06 BF = 8.79
Other > Self	1	R. Lateral occipital cortex, superior	52-68 20	1494	r = .26 BF = 1.45	r = .05 BF = 8.88	r = -.004 BF = 9.62	r = .065 BF = 8.57
	2	Precuneus/PCC	4-66 32	1058	r = .31 BF = 0.63	r = -.12 BF = 6.47	r = .05 BF = 9.05	r = .03 BF = 9.38
	3	L. Lateral Occipital cortex, superior	-48-66 22	673	r = .32 BF = 0.55	r = .04 BF = 9.17	r = -.017 BF = 9.55	r = .10 BF = 7.26
	4	L. Middle temporal gyrus, anterior	-56-12-18	561	r = .11 BF = 6.85	r = -.14 BF = 5.53	r = .02 BF = 9.52	r = -.18 BF = 4.06
	5	R. Middle temporal gyrus, anterior	60-2-28	526	r = .18 BF = 4.04	r = -.11 BF = 6.86	r = .02 BF = 9.49	r = -.12 BF = 6.46
	6	R. Lateral Middle Temporal Gyrus	64-44-12	249	r = .16 BF = 4.93	r = -.12 BF = 6.39	r = .006 BF = 9.61	r = .006 BF = 9.61

distribution of r-values and Bayes factors for each of the correlations. r = Pearson r correlation coefficient. BF = Bayes factor. L = left. R = right. PCC = posterior cingulate cortex

<https://doi.org/10.1371/journal.pone.0216182.t002>

individuals who had more specific patterns of ongoing thought. These spatial maps both overlapped within the caudal posterior cingulate (shown in yellow in the inset of Fig 4). Notably, this region was shown to have heightened connectivity with a region of the parahippocampus for meta-cognitive aspects of mind-wandering experiences in a study by [40]. No such relationship was found for the extent of memory related content during mind-wandering. This correspondence between neural evidence from the domain of connectivity and task-based fMRI, and across research groups, provides converging evidence of a link between this posterior node in the DMN with relatively abstract aspects of ongoing thought, rather than particular aspects of its content. In order to place this region of caudal posterior cingulate in a broader cortical context, we examined its intrinsic connectivity architecture using resting-state data collected in the larger sample. Functional connectivity analyses revealed a pattern of correlation with many of the structures in the DMN including the posterior cingulate cortex, ventromedial prefrontal cortex, medial and lateral temporal cortex and angular gyrus (see the grey panel in Fig 4). Comparison of this pattern of functional connectivity with maps of regions modulated by the nature of the referent during trait judgements (Self > Other and the reverse) revealed that all but one region (lateral occipital cortex) fell within the connectivity map of this region. This was confirmed by a formal conjunction of the three maps (see the right hand inset).

In sum, our study found little evidence of an association between the neural processing during Self or Other focused mentation and patterns of similar themed ongoing thought in the laboratory. Neural engagement during Self and Other trait processing, was not correlated to reports of off-task content, despite PCA highlighting these topics as characteristic themes of this state (i.e., when participants report they are not engaged in the task they often report they are instead thinking about themselves or others). Instead activity in a caudal aspect of the

posterior cingulate during self-reference was linked to the level of subjective detail in experiences in the lab. This pattern of results is difficult to reconcile with a view of the relationship between off-task thought and the DMN as due to hyper responsiveness to forms of content that often make up patterns of spontaneous off-task episodes. The absence of an association with off-task thought cannot be easily attributed to a lack of power in our study, since our Bayesian analysis suggests that the evidence in favour of the null hypothesis is reasonably strong. Likewise they cannot be discounted by virtue of a lack of sensitivity of the task focus component produced through our method of analysis (i.e. MDES), since broadly equivalent patterns of experience, generated by the same method, vary with objective measures including neural [18] and pupillometric [25] data.

Discussion

While our data are inconsistent with a simple role for the DMN in self-relevant content of off-task thought, they do not exclude a role in broader features of cognition, such as its detail or meaning. For example, a role of the DMN in experiences with high levels of subjective detail draws support from studies probing the mechanics of cognition in tasks, especially those in the domain of memory which are both thought to be related to patterns of ongoing thought (e.g. [19]). For example, patterns of activity within the posterior core of the DMN (including the caudal area highlighted in our analysis) describe the vividness of episodic retrieval [42]. Neuro-stimulation is difficult in medial regions of the DMN, however, studies show that disrupting function in lateral aspects of the DMN within the angular gyrus impair source monitoring and confidence of episodic memory [43], and, in the semantic domain, impairs specific retrieval but not more difficult patterns of retrieval [44]. Importantly, other studies from multiple different research groups identified associations at rest between the posterior cingulate region and medial lobe regions and more abstract elements of ongoing thought such as how specific it is or its meta cognitive complexity (e.g. [19, 45]).

A role of the DMN in supporting broad features of cognition, such as the level of subjective detail, is consistent with neuroanatomical evidence situating this system as an integrative core located at the top of a neurocognitive hierarchy, with the region of pCC identified in our study close to the apex [16]. This topographical organisation is assumed to allow transmodal regions to be less tethered to specific modalities of input and so better able to integrate from a broader range of cortical inputs [46]. Accordingly the capacity of regions such as the posterior cingulate to draw on neural signals from a wide range of cortical regions [47], could enable it to support more elaborate and detailed mental representations. Similarly, regions of the pCC have also been ascribed an important role in a process that is often described as scene construction [48]. In the context of these observations, the current data provide additional evidence supporting a role for the DMN in broader features of cognition, such as how it is being represented, rather than more local features such as what it is about [19, 49]. The pCC may be particularly important for this process because studies have shown that this region of cortex contains echoes of multiple different regions, including those outside of the DMN [50, 51, 52]. A recent analysis of the found that greater grey matter structure of the cortex in posterior regions of the para-hippocampus were associated with more detailed experiences in the laboratory a region that had strong connectivity with both the angular gyrus and the posterior cingulate [53].

Prior observations of DMN activity within the off-task state [7, 54], may, therefore have been at least partially mischaracterised. Rather than reflecting the act of processing particular aspects of content, the recruitment of structures within the DMN may describe patterns of ongoing thought with particular features, such as whether they have vivid, absorbing details.

This mischaracterisation may have emerged for methodological reasons. As we have done, many prior studies measure the contents of ongoing thought in the context of tasks with limited semantic or self-relevant content, and often with few cognitive demands. Under these conditions, being on-task may be boring and dull, while when we are off-task we can generate imaginative experiences that can vary from states of task focus in many different aspects [55]. This can make simple binary comparisons of neural activity in different states, such as on- versus off-task experiences, complex to interpret because it is unclear which differences in the nature of ongoing experience are related to which neural patterns.

We overcame this limitation in the current study by sampling neural function in a relatively engaging self-reference task and associating this with self-reports of experience in the lab. This allows neural processing to be described in a context when participants engage relatively well-specified cognitive operations and so allows for a more mechanistic constraint on interpretations of the functions of neural processing than would be possible during unconstrained states. We also measured multiple features of ongoing thought, while studies typically focus on only a few aspects of experience, often using a series of forced binary choices (e.g. on- vs. off-task). Although there are clear methodological advantages to simple experience sampling regimes, such as efficiency, they are less well suited to probing specific nuances of the complex landscape of ongoing thought. Our approach overcomes this problem by measuring experience along multiple dimensions and examining the latent structure contained by these data.

However, complex experience sampling with multiple items has weaknesses [2]—it is time consuming, and may lead to concerns of lack of validity given its intrusiveness or reactivity [56]. Fortunately some of these issues can be addressed by measurements made across multiple studies. For example, in the current study we acquired neural activity during Self and Other judgements and related these to experience measures recorded in the lab, while in our prior experiment ongoing neural activity was related to online measures of experience sampling [18]. As both studies implicated the DMN in patterns of detailed ongoing thought, we can be confident that this conclusion does not rest on a feature unique to only one method—such as momentary changes in neural function occurring because of the momentary load induced by experience sampling [56]. Likewise, evidence that on-line measures of experience identified both aspects of experience (i.e., off-task thought and subjective detail) are linked to neural signals (i.e. [18]), rules out accounts of the current data as simply emerging because different features of experience vary in their memorability. Moving forward, it seems likely that accurately describing associations between neural function and ongoing thought, requires the characterisation of multiple dimensions of experience and the development of the methodological tools that enable this heterogeneous landscape to be explored in different situations [1, 6]. It is also important to consider whether our data has sufficient power to detect the effects that it did. Based on our sample size $N = 65$, we have an 80% power to detect correlations in the .34 range and above [57]. The correlations identified in our ROI analyses were slightly below this level (in the range of .26-.31). Although our sample of 65 is relatively high for a task-based fMRI experiment and was able to detect significant brain to experience associations, future studies of individual differences in neural function may wish to consider using a larger sample size to ensure the robustness of their effects. In this vein, it is important to note that our study did not find differences between self or other relevance were related to patterns of experience in the laboratory. It is possible that this pattern emerges because the region of the posterior cingulate cortex highlighted plays a general role in both conditions identified by our study, however, it remains a possibility that with a greater sample size we would have been able to resolve these conditional differences.

In conclusion, our study did not find support for the hypothesis that patterns of off-task thought are linked to hyper responsiveness within the DMN to social or personally relevant

information. Instead, we found that experiences with high levels of subjective detail in the lab, were associated with greater activity in the pCC when thinking about another person. This pattern of results is not consistent with an account of states of off-task mind-wandering as resulting from a hyper responsivity of the DMN to personally relevant or social content. Instead these data add to an emerging picture of the DMN as playing an important role in more general aspects of cognition such as the subjective detail in experience. Moving forward, one question that emerges from this work is whether the DMN plays an important role in the level of subjective detail in off task states, that complements its apparent role in active tasks states (i.e. [18]).

Supporting information

S1 Fig. Scree plot describing the decomposition of experience sampling data in the lab for all 207 participants (A) and for a subset of these (N = 65) who took part in the self-reference task (B). In both decompositions the first four components revealed a significant positive correlation (PCA1 –Detail; $r = .69$, $p = .009$; PCA2 –Off-task; $r = .72$, $p = .005$; PCA3 –Modality; $r = .94$, $p < .001$; PCA4 –Emotion; $r = -.65$, $p = .02$).
(TIFF)

S2 Fig. Heat maps describing the decomposition of experience sampling data in the lab for all 207 participants (left) and for a subset of these (N = 65) who took part in the self-reference task (right). Correlations between the maps revealed a significant relationship between each component across the two datasets (PCA1 –Detail; $r = .69$, $p = .009$; PCA2 –Off-task; $r = .72$, $p = .005$; PCA3 –Modality; $r = .94$, $p < .001$; PCA4 –Emotion; $r = -.65$, $p = .02$).
(TIFF)

S3 Fig. Conjunction of Other>Self whole-brain map (cool colour; Fig 2) and Self>Rest regressed against Detail component (warm colours; Fig 3) reveals cluster in caudal posterior cingulate cortex.
(TIFF)

S4 Fig. Warm colours highlight regions showing more activity during task (Self and Other judgements) compared to rest. The spatial maps are thresholded at $Z = 3.1$ and are controlled for multiple comparisons ($p < .05$, FWE).
(TIFF)

S5 Fig. Functional connectivity of intracalcarine seed taken from Other>Rest regressed against detail component (Fig 2). All reported clusters were corrected for multiple comparisons using the Family-Wise Error (FWE) detection technique at the .05 level of significance (uncorrected at the voxel-level, .001 level of significance).
(TIFF)

S1 Table. Location of peak coordinates from the univariate contrasts of Self > Other and Other > Self.
(DOCX)

S2 Table. Location of peak coordinates from the univariate contrasts of Self and Other regressed against the PCA loadings from the MDES.
(DOCX)

Author Contributions

Conceptualization: Charlotte Murphy, Mladen Sormaz.

Data curation: Charlotte Murphy, Giulia Poerio, Mladen Sormaz, Hao-Ting Wang, Deniz Vatansever.

Formal analysis: Charlotte Murphy, Giulia Poerio, Hao-Ting Wang, Micah Allen, Jonathan Smallwood.

Funding acquisition: Elizabeth Jefferies, Jonathan Smallwood.

Investigation: Charlotte Murphy, Mladen Sormaz.

Methodology: Charlotte Murphy, Mladen Sormaz, Micah Allen, Daniel S. Margulies, Jonathan Smallwood.

Project administration: Charlotte Murphy.

Resources: Daniel S. Margulies.

Supervision: Charlotte Murphy, Elizabeth Jefferies, Jonathan Smallwood.

Validation: Charlotte Murphy, Micah Allen.

Visualization: Charlotte Murphy, Hao-Ting Wang, Jonathan Smallwood.

Writing – original draft: Charlotte Murphy, Elizabeth Jefferies, Jonathan Smallwood.

Writing – review & editing: Charlotte Murphy, Giulia Poerio, Mladen Sormaz, Deniz Vatansever, Daniel S. Margulies, Jonathan Smallwood.

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