Macro-scale patterns in functional connectivity associated with ongoing thought patterns and dispositional traits

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Abstract

Complex macro-scale patterns of brain activity that emerge during periods of wakeful rest provide insight into the organisation of neural function, how these differentiate individuals based on their traits, and the neural basis of different types of self-generated thoughts. Although brain activity during wakeful rest is valuable for understanding important features of human cognition, its unconstrained nature makes it difficult to disentangle neural features related to personality traits from those related to the thoughts occurring at rest. Our study builds on recent perspectives from work on ongoing conscious thought that highlight the interactions between three brain networks - ventral and dorsal attention networks, as well as the default mode network. We combined measures of personality with state-of-the-art indices of ongoing thoughts at rest and brain imaging analysis, and explored whether this 'tri-partite' view can provide a framework within which to understand the contribution of states and traits to observed patterns of neural activity at rest. To capture macro-scale relationships between different brain systems, we calculated cortical gradients to describe brain organisation in a low dimensional space. Our analysis established that for more introverted individuals, regions of the ventral attention network were functionally more aligned to regions of the somatomotor system and the default mode network. At the same time, a pattern of detailed self-generated thought was associated with a decoupling of regions of dorsal attention from regions in the default mode network. Our study, therefore, establishes interactions between attention systems and the default mode network are important influences on ongoing thought at rest and highlights the value of integrating contemporary perspectives on conscious experience when understanding patterns of brain activity at rest.

Introduction

Macro-scale patterns of brain activity at rest have the potential for understanding the organisation of neural function, different types of psychiatric conditions (Cao et al., 2018; Koban et al., 2021), developmental changes including those during adolescence and old age (Dosenbach et al., 2010; Cui et al., 2020; Gratton et al., 2020; Wen et al., 2020), neurological disorders (Zhang et al., 2021) and are important for revealing the neural basis behind the landscape of self-generated experiences (Karapanagiotidis et al., 2019; Mckeown et al., 2020; Kucyi et al., 2021). However, compared to controlled experimental conditions, interpreting neural activity recorded during resting-state functional magnetic resonance imaging (rs-fMRI) is challenging, partly because both trait-level aspects of the individual, and, the inherently complex and dynamic nature of ongoing experience at rest are both contributory factors to the observed brain activity (Smallwood et al., 2021b). It has recently been suggested that the meaning of different patterns of neural activity can be usefully constrained by pairing imaging data at rest with additional measures (Finn, 2021), for example by accounting for the patterns of thoughts individuals experience at rest (Karapanagiotidis et al., 2020, 2021; Mckeown et al., 2020; Gonzalez-Castillo et al., 2021; Kucyi et al., 2021) or features of their personality (Hsu et al., 2018). While this methodological perspective is invaluable, we currently lack a theoretical framework within which to understand the brain-cognition relationships that these observations will establish. To address this gap in the literature, our study explores whether contemporary theories of the neural basis of ongoing conscious thought can provide a framework within which to interpret associations between macro-scale patterns of neural activity observed at rest, and measures of traits and ongoing experience.

Emerging views of how the brain supports patterns of ongoing conscious thought highlight interactions between three large scale networks (Menon et al., Smallwood et al., 2021; Huang et al., 2021): the ventral attention network (VAN), the dorsal attention network (DAN) and the default mode network (DMN)[⊕]. According to these ‘tri-partite’ network accounts, key hubs of the ventral attention network, such as the anterior insula and dorso-lateral prefrontal cortex, help gate access to conscious experience, influencing interactions between the DAN, which is more important for external mental content (Corbetta and Shulman, 2002), and the DMN which is important when states rely more on internal representations (Smallwood et al., 2021a). For example, Huang and colleagues established that activity levels in the anterior insula determine whether stimuli presented at perceptual threshold are consciously perceived (Huang et al., 2021), and this gating of external input emerged as a consequence of changes in the normal interactions between the DAN and DMN. They also found that disruptions to activity in the insula through anaesthesia resulted in reductions in self-generated mental imagery. Coming from a different perspective, Turnbull and colleagues (Turnbull et al., 2019b) used experience sampling during task performance to link patterns of neural activity to different features of ongoing thought. For example, they found activity in the dorsolateral prefrontal cortex (a member of the VAN, (Yeo et al., 2011)) was correlated with apparently contradictory patterns of ongoing thought – (i) self-generated episodic thoughts during periods of low demands, and (ii) patterns of detailed task focus when individuals were engaged in demanding external task. In the same study, neural activity within regions of the dorsal parietal cortex within the DAN, was exclusively reduced when participants engaged in self-generated thinking, highlighting a parallel neglect of external input seen by Huang and colleagues. Finally, in a second study, Turnbull and colleagues found that at rest, trait variance in the ability to focus on self-generated experience in laboratory situations with lower task demands is associated with decoupling of signals arising from the DAN and DMN (Turnbull et al., 2019). Summarising this emerging evidence, studies focused on understanding ongoing thought patterns from different perspectives converge on the view that regions of the VAN may be important for gating conscious access to different types of content by biasing interactions between the DAN and the DMN (Huang et al., 2021; Smallwood et al., 2021b)

[⊕] In this paper we refer to the networks using the taxonomy provided by Yeo, Krienen and colleagues (Yeo et al., 2011)

Our current study explored whether this "tri-partite network" view of ongoing conscious thought derived from studies focused on understanding conscious experience, provides a useful organising framework for understanding the relation between observed brain activity at rest and patterns of cognition/ personality traits. We examined links between both (i) trait descriptions of individuals and (ii) patterns of ongoing thought. Our sample was a cohort of 144 participants who underwent a one-hour resting-state scan. Across this one-hour period, participants were interrupted on four occasions to answer a set of questions about their experiences at rest using multidimensional experience sampling (MDES), similar to a number of prior neuroimaging studies (Smallwood et al., 2016; Poerio et al., 2017; Wang et al., 2018). During a different session, the same participants also completed a battery of measures assessing features of their personality (such as the Big five (Costa and McCrae, 2008)) as well as subclinical/ psychiatric traits such as trait anxiety and depression (Zigmond and Snaith, 1983). Since our research question depends on understanding the hypothesised relationship between large scale networks (VAN, DMN and DAN), we used the Brainspace toolbox (Vos de Wael et al., 2020) to provide whole brain low dimensional representations of functional brain organisation, generating maps which represent the similarities and differences in the activity within different systems. We used R version 4.2.0 (R Core Team, 2021) to produce low dimensional representations of both traits and thoughts using principal component analysis (PCA). Using these two sets of data, we performed multiple regression to identify how brain network organisation varies with traits and states. In these analyses, the low dimensional representations of brain organisation were the dependent measures, and the components of traits and states were explanatory variables.

Methods

Data

The dataset used here is part of the MPI-Leipzig Mind-Brain-Body (MPILMBB) database (Mendes et al., 2019). The complete dataset consists of a battery of self-reported personality measures, measures of spontaneous thought, task data, and structural and resting-state functional MRI (one hour, divided into four adjacent 15-min sessions) from participants between 20 and 75 years of age. A detailed description of the participants, measures, and data acquisition protocol has been previously published along with the dataset (Mendes et al., 2019).

Participants

We limited our investigation to personality and thought self-reports, and rs-fMRI from participants under 50 years of age, who had complete data from at least three resting-state scans. The resulting sample included 144 participants (74 men, mean age= 26.77 years, SD= 4.03; 70 women, mean age = 26.93 years, SD = 5.55).

Resting state fMRI

The current sample includes fully pre-processed rs-fMRI data from 144 participants (four scans from 135 participants, and three scans from nine participants whose data were missing or incomplete). The rs-fMRI was acquired in axial orientation using T2∗-weighted gradient-echo echo planar imaging (GE-EPI) sensitive to blood oxygen level-dependent (BOLD) contrast. Sequences were identical across the four runs, with the exception of alternating slice orientation and phase-encoding direction, to vary the spatial distribution of distortions and signal loss. Imaging and pre-processing parameters are described in detail in Mendes et al (Mendes et al., 2019).

Personality measures

To provide a broad description of individual traits we included data from the following 21 questionnaires:

Table 1. List of personality/ dispositional trait questionnaires

Abbreviation	Behavioural Measure
ACS	Attention Control Scale (Derryberry and Reed, 2002)
ASR	Adult Self Report (Achenbach and Rescorla, 2003)

BDI-II	Beck Depression Inventory -II (Beck et al., 1993)
BIS/BAS	Behavioural Inhibition and Approach System (Carver and White, 1994)
BP	Boredom Proneness Scale (Farmer and Sundberg, 1986)
ESS	Epworth Sleepiness Scale (Johns, 1991)
Gold-MSI	Goldsmiths Musical Sophistication Index (Müllensiefen et al., 2014)
HADS	Hospital Anxiety and Depression Scale (Zigmond and Snaith, 1983)
IAT	Internet Addiction Test (Young, 1998)
IMIS	Involuntary Musical Imagery Scale (Floridou et al., 2015)
MMI	Multimedia Multitasking Index (Ophir et al., 2009)
NEO PI-R	NEO Personality Inventory-Revised (Costa and McCrae, 2008)
PSSI	Personality Style and Disorder Inventory (Kuhl and Kazén, 2009)
SCS	Brief Self-Control Scale(Tangney et al., 2004)
SDS	Social Desirability Scale-17 (Crowne and Marlowe, 1960)
SES	Self-Esteem Scale (O'Malley and Bachman, 1979)
SD3	Short Dark Triad (Jones and Paulhus, 2014)
S-D-MW	Spontaneous and Deliberate Mind-Wandering (Carriere et al., 2013; Golchert et al.,
STAXI	State-Trait Anger Expression Inventory
TPS	Tuckman Procrastination Scale (Tuckman, 2016)
UPPS-P	UPPS-P Impulsive Behaviour Scale (Lynam et al., 2006; Schmidt et al., 2008)

Multi-dimensional experience sampling

Participants underwent a short MDES survey immediately after each 15 min rs-fMRI scan, which retrospectively measured various dimensions of spontaneous thought. The battery included 12 statements which participants rated on a visual analog scale with 5% response increments that go from 0% = "describes my thoughts not at all" to 100% = "describes my thoughts completely". The current analysis sample includes MDES data for all available instances of rs-fMRI scans for each participant.

Analyses

Dimension reduction for questionnaire and MDES data

We performed two separate principal component analyses (PCA) to obtain low dimensional summaries of the 71 trait variables from 21 questionnaires, and 12 thought variables from MDES.

71 scores from the personality questionnaires of 144 participants were included and missing data were imputed by the variable mean. PCA was performed on this matrix and five "trait" components (henceforth referred to as "traits") were selected on the basis of eigenvalues >1, using the Kaiser-Guttman criterion (Joliffe, 2002). For the MDES data, separate instances of responding for each participant were concatenated, resulting in a matrix with 576 observations of 12 variables. PCA was performed on this matrix, and five "thought" components (henceforth referred to as "thought patterns") were selected on the basis of eigenvalues >1. Varimax rotation was applied to both solutions to optimize the distinctiveness of each component. The five thought pattern scores were then averaged across the four scans, resulting in one score for each thought pattern for each participant, describing their location on a particular thought dimension.

Dimension reduction for whole-brain functional connectivity

Functional time-series for each participant was extracted using the Schaefer 400 parcellation (Schaefer et al., 2018) using the fully pre-processed data from all resting-state scans. The data from separate scans were concatenated, and a 400x400 connectivity matrix was calculated from the resulting time series for each participant using Pearson correlation. A group connectivity matrix of the whole sample was calculated by averaging the 144 individual matrices.

In order to summarize whole brain connectivity in a low-dimensional space, we performed gradient analysis using the Brainspace toolbox (Vos de Wael et al., 2020). 10 macro-scale gradients were calculated for the group (Fig 2). First, we applied fisher's z transform to the group matrix, building an affinity matrix (kernel= normalized angle, sparsity= 0.9) and then decomposed it using PCA. We chose the PCA approach for gradient calculation, as Hong and colleagues (Hong et al., 2020) have shown that compared to non-linear decomposition methods, PCA provides better reliability and higher phenotypic predictive value for connectivity gradients. For ease of interpretation and comparability, group gradients were aligned to a subsample of the HCP dataset (Essen et al., 2013) included in BrainSpace. Finally, following Mckeown et al. (Mckeown et al., 2020) 10 gradients were calculated in order to maximize the gradient fit for all individuals during alignment. Individual gradients were calculated for each participant, aligned to the group-level gradients, resulting in a 400x10 matrix for each participant. Subsequent regression analyses were limited to the first three gradients, which have been relatively well-characterized in previous work (Margulies et al., 2016; Mckeown et al., 2020; Turnbull et al., 2020). To visualize the functional axis captured by each gradient, we performed Neurosynth (Yarkoni et al., 2011) decoding on the group gradient maps (Fig 2). Further, we calculated the average gradient score for all parcels within each of the seven connectivity networks described by Yeo and colleagues (Yeo et al., 2011) (Fig 2).

Stability of thoughts-patterns and gradients

To quantify the stability of thoughts and connectivity gradients over the whole scanning period, intra-class correlation coefficients (ICC) were calculated for the thought patterns and following Hong and colleagues (Hong et al., 2020), discriminability indices (Bridgeford et al., 2021) were calculated for whole gradients by treating the 4 scans and subsequent thought probes as separate instances. We used the two-way mixed effects model (i.e. type 3 ICC) used for quantifying test-retest reliability, where samples cannot be considered independent (Koo and Li, 2016). Only the 135 participants who had four full-length resting state scans were included in this analysis. As this analysis found reasonable levels of reliability (see below), the averages of the four separate thought scores were used as regressors in subsequent analysis. This allowed for both a robust measure of thought patterns over the whole testing period, and the inclusion of all 144 participants in the analysis.

Multiple Multivariate Regression

To investigate the relationship between individual differences in traits, thoughts, and macro-scale cortical gradients, we used multiple multivariate regression as implemented in the MATLAB SurfStat Toolbox (Worsley et al., 2009) [http://www.math.mcgill.ca/keith/surfstat/]. 400 separate linear models were estimated for 400 parcels, with the gradient scores from the first three gradients as the dependent variables, and with five trait scores (Fig 1A) and five thought scores (Fig 1B), as well as nuisance variables age, motion, and gender included as independent variables. The resulting significant effects from 400 parcels were corrected for False Discovery Rate (FDR, $q < .05$) (Storey, 2003) at the multivariate (three gradients) level. Follow-up univariate analyses were performed on the resulting parcels for each gradient separately, and effects were further Bonferroni corrected ($p_{bonf} < .025$) for the total number of comparisons performed for all parcels (including the analyses of all three gradients) for each variable. Additionally, to see how the trait components related to the thought components, we performed multiple multivariate regression with the thoughts as dependent variables and traits as independent variables.

Results

Traits and thought patterns

Application of PCA to the battery of personality questionnaires resulted in five “traits” (Fig 1 A) with eigenvalues > 1, explaining 48.4% of the variance. The five trait components, independent of the direction of loadings, largely map onto the “big five” personality factors: neuroticism, conscientiousness (positive loading on “procrastination” in our PCA result), extraversion (positive loading on “introversion” in our PCA result), agreeableness (positive loading on anti-social in our results) and openness to experience, respectively, with the first component “neuroticism” accounting for 23.7% of the total variance. Application of PCA to the

MDES questions revealed five “thought patterns” (Fig. 1 B) with eigenvalues>1, explaining 65.4% of the variance. Based on the most heavily loaded dimensions within each pattern, we named these: “modality” (image vs words), “positive episodic social”, “specific internal”, “self-relevant” and “prospective”.

Intraclass correlation – thoughts

Our first analysis established the reliability of thought components across the one hour of scanning. The five thought patterns showed low to moderate agreement between individual scores from single sessions (modality = 0.5856, positive episodic-social= 0.4531, specific internal= 0.5226, self-relevant = 0.5832, prospective= 0.3118), indicating a degree of variability between sessions. The average of all scores had high ICCs for the first four components (modality = 0.8497, positive episodic social = 0.7783, specific internal = 0.8141, self-relevant = 0.8484, prospective = 0.6444). The average scores from 4 sessions were used as regressors in subsequent analyses.

Next, we examined the relationship between the low dimensional representations of both personality and thoughts. Multiple multivariate regression using traits as predictor variables of thought patterns established that “negative affect” had a significant effect on thoughts $(_{5,134}) = 3.88$, $p = 0.003$, partial $\eta^2 = 0.127$). Univariate follow-up showed that a high score on trait neuroticism was significantly associated with less “positive episodic social” thought (pattern 2; ß = -0.229, 95% CI = [-0.389 -0.07], $p = 0.005$, partial $\eta^2 = 0.055$) as well as greater “self-relevant” thought (pattern 4; ß = 0.229, 95% CI = [0.066 0.391], $p = 0.006$, partial $\eta^2 = 0.053$), (Supplementary Fig. 3).

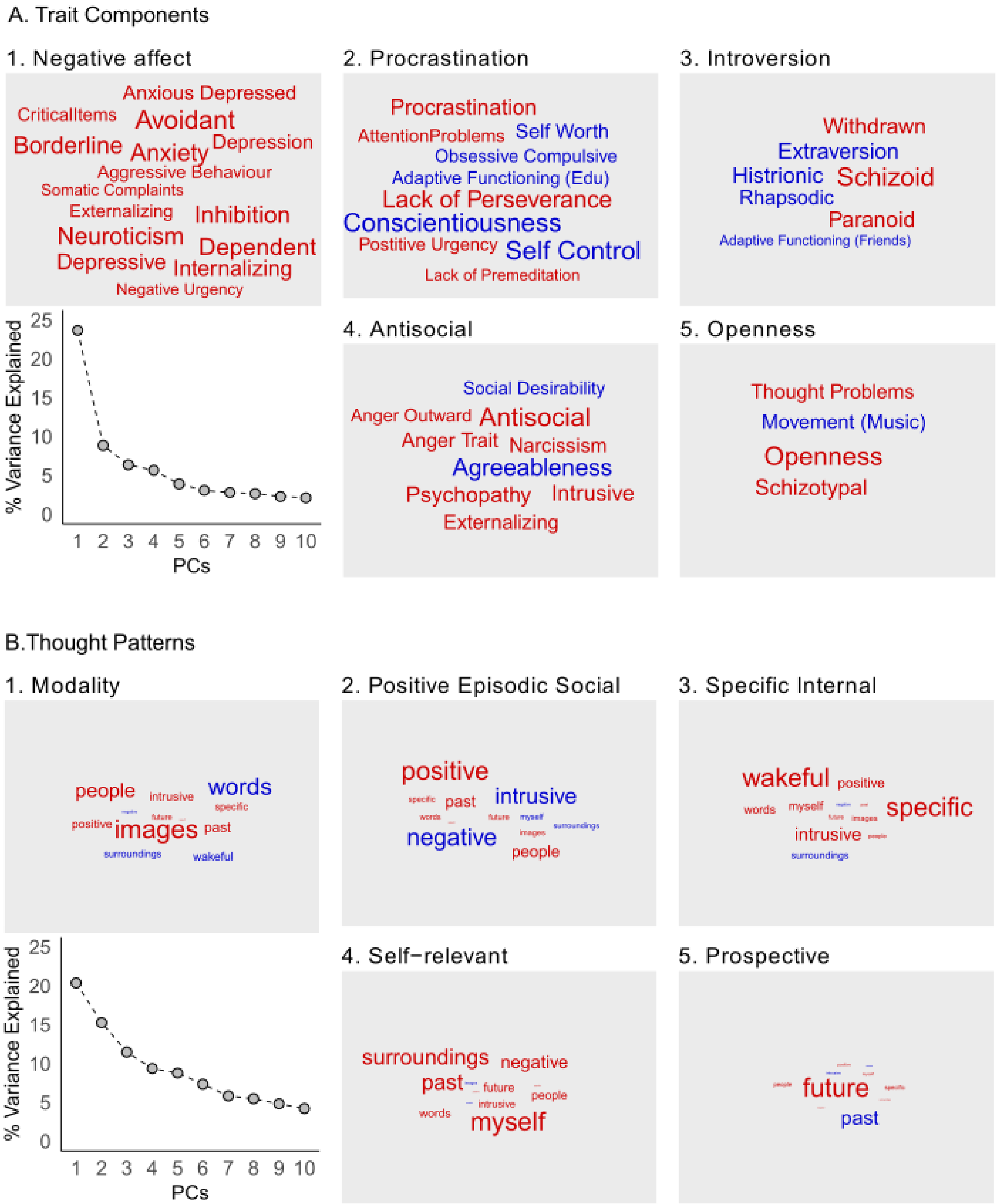

Figure 1. Principal components of traits and thoughts

A) First five trait components derived from PCA are represented as word-clouds with negative loadings shown in blue, and positive loadings in red; the absolute loading value is represented by the font size of the item. In the bottom left panel, scree-plot showing the percentage of trait variance explained by the each of the first 10 components **B)** Results of the application of PCA to the MDES data, depicted in the same way.

Macro-scale cortical gradients

The first three group level gradients are shown in Fig. 2 along with their Neurosynth meta-analytic associations and relationships to the Yeo-networks (Yeo et al., 2011) (7-network solution). The first gradient (G1) differentiates between visual regions at one end and DMN at the other. The second gradient (G2) describes the dissociation between somatomotor and visual cortices. The third gradient (G3) captures the segregation between different transmodal systems (the default mode network versus the fronto-parietal system). The three gradients are largely similar to the ones reported by Margulies et al.(Margulies et al., 2016) and subsequent literature (Hong et al., 2019; Paquola et al., 2019; Bethlehem et al., 2020; Mckeown et al., 2020; Turnbull et al., 2020). The endpoints of G1 are different in that one end is anchored by the visual network alone, as opposed to visual and somatomotor, while in G2, the somatomotor network is separated from both the visual and default mode networks, as opposed to the visual network alone. For ease of interpretation and comparability with previous studies (Mckeown, Turnbull), gradients were aligned to a subsample of the HCP dataset (Essen et al., 2013) included in BrainSpace. Similar to this template, the first two gradients together describe network-level connectivity space, anchored at three ends by the visual, somatomotor and default mode network, respectively (Fig. 3). Single gradients tended to be stable over the 4 sessions, with a discriminability index of 0.964 for Gradient 1, 0.918 for Gradient 2, and 0.983 for Gradient 3 over four adjacent scans from 135 participants. Discriminability indices are similar to those previously reported by (Hong et al., 2020).

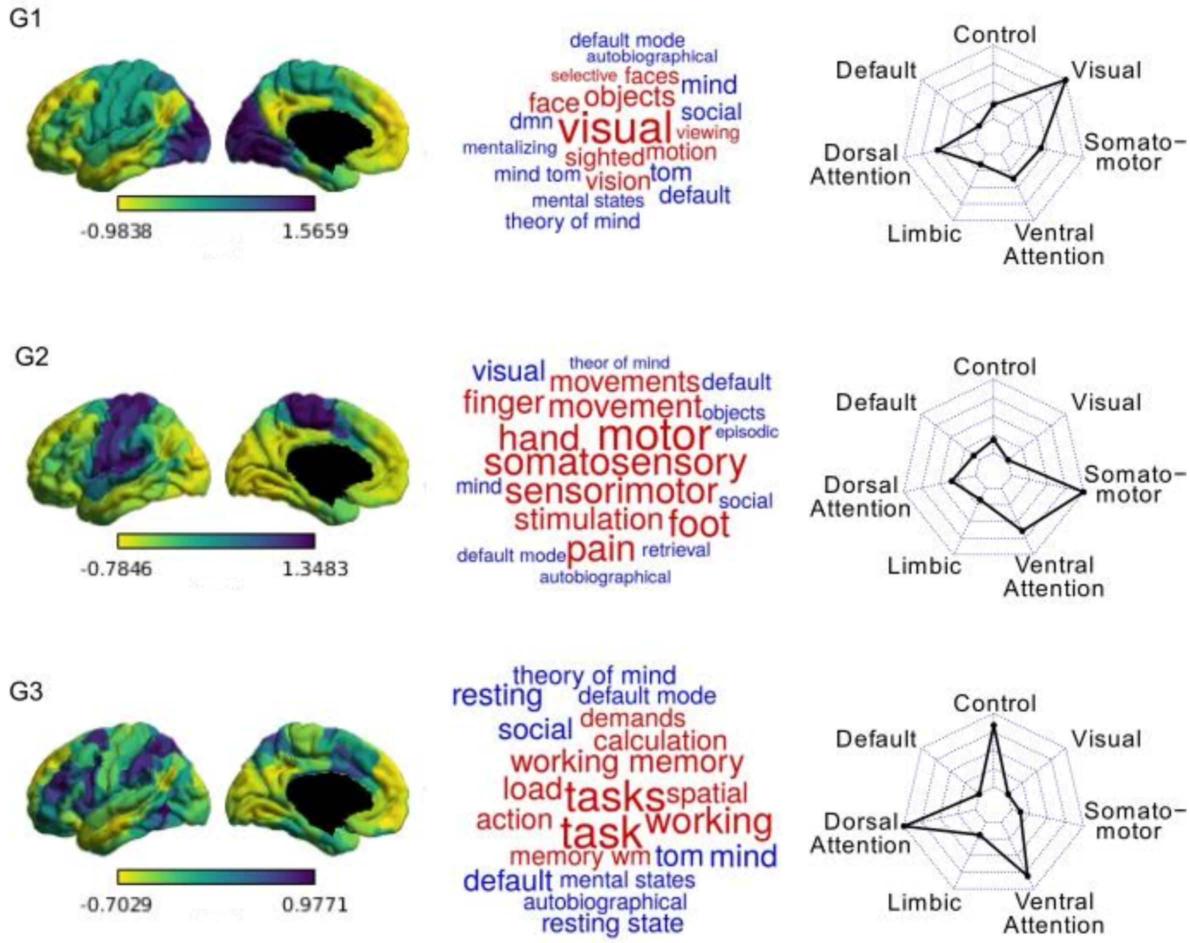

Figure 2. Group-level gradients of functional connectivity

On the left are the first three group-averaged gradients, represented in left lateral and medial views. Regions with similar whole-brain connectivity profiles are shown in similar colours, with yellow and purple regions indicating most dissimilar connectivity patterns. Loading ranges and directions are arbitrary. In the middle, word clouds representing the top 10 positive (red) and negatively correlated (blue) Neurosynth decoding topic terms for each gradient map. On the right, radar-plots showing the Yeo-network profile of each group-level gradient depicted in the left column. Each radar-plot shows the mean gradient loadings for all parcels within the seven Yeo networks.

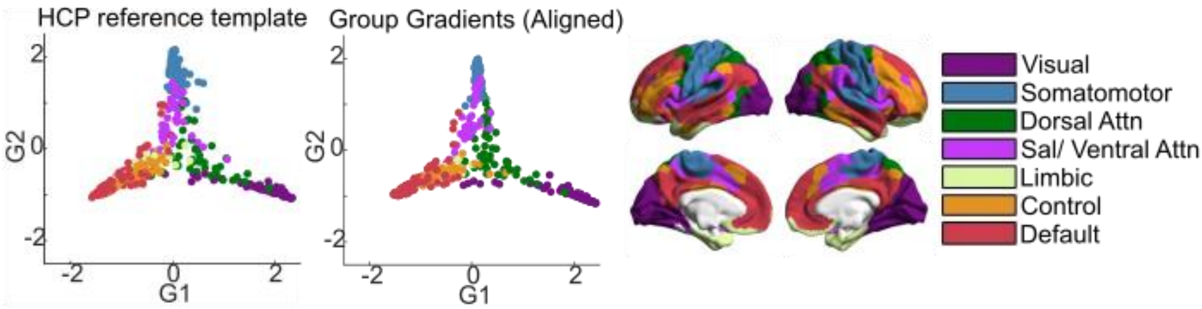

Figure 3. Comparison of group-level gradients to BrainSpace HCP template

The first scatterplot shows 400 parcel positions along G1 and G2 in the template calculated from the HCP subsample included in BrainSpace toolbox (Vos de Wael et al., 2020). The second scatterplot shows parcel positions in the group-level gradients G1 and G2 after Procrustes alignment to the HCP template. Parcels are color-coded according to their respective Yeo network. Yeo networks are shown as color-coded brain maps on the right.

Relationship between state- trait variability and cortical gradients

Having established low dimensional representations of thought, personality, and brain organisation, we next examined associations between different types of personality and ongoing thought experienced during the scan and our metrics of functional brain organisation. To this end, we performed a multiple multivariate regression with thoughts, traits, and nuisance variables (motion, age and gender) as independent variables, with whole brain functional organisation, as captured by the first three gradients, as dependent variables. In these analyses both trait "introversion" and a pattern describing "specific internal" thought showed significant effects at the multivariate level. Results from the univariate follow-up of effects within each gradient are shown in Fig. 4 and 5, and Table 2.

<u>Trait Introversion (Fig 4)</u>

Along the first gradient, a parcel within the right orbitofrontal cortex (within the executive control network, shown in orange) showed more similarity with transmodal regions for individuals high on introversion. Six parcels within the ventral attention network, including anterior insula, operculum and cingulate cortex were closer to the somatomotor end along gradient two (shown in purple). The same regions showed lower scores along the third gradient in participants with higher introversion scores, indicating stronger integration with the default mode network. A parcel within posterior cingulate cortex (control) was also more segregated from the visual end of gradient two in participants with higher introversion scores.

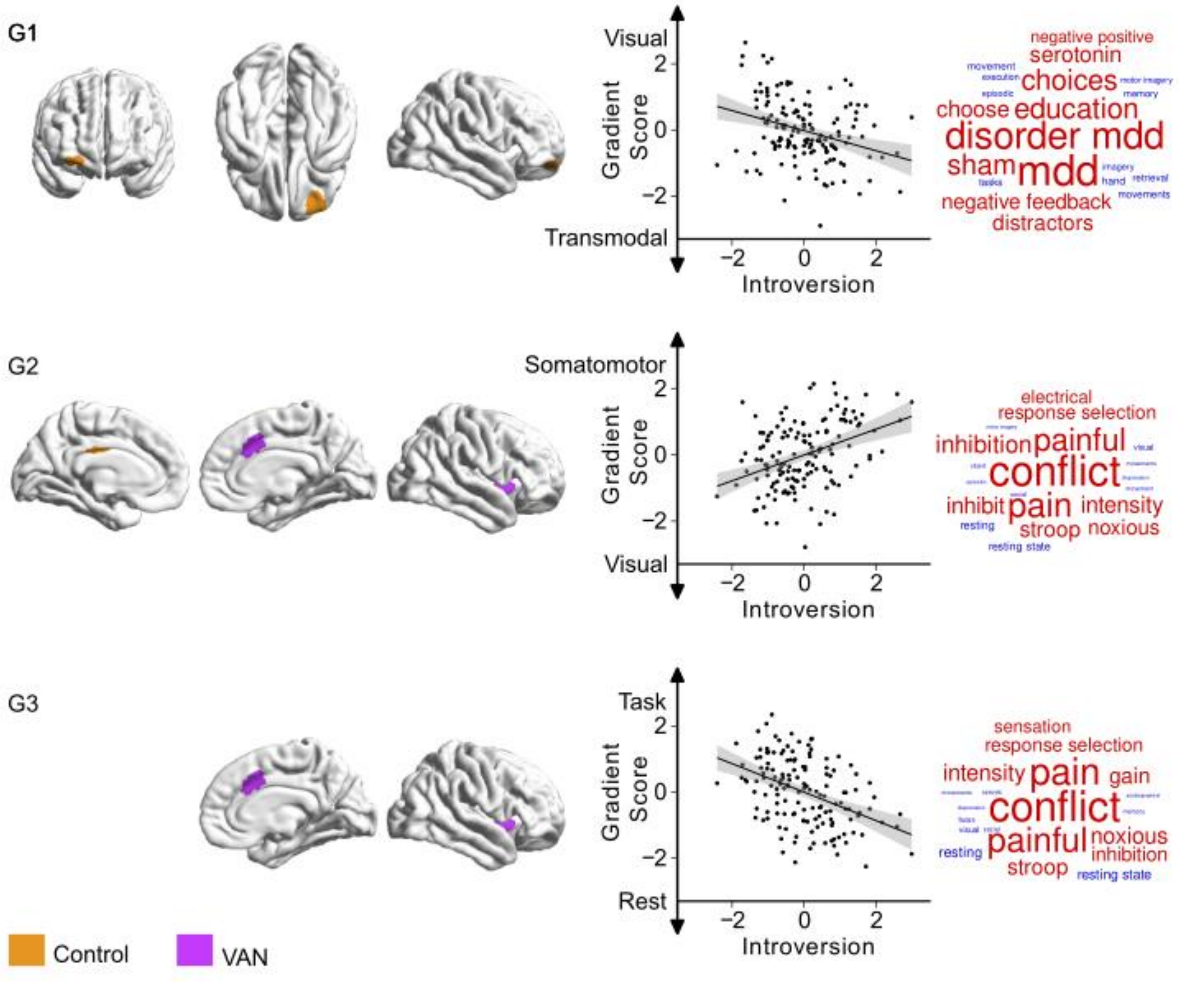

Figure 4. Relationship between trait "Introversion" on the first three connectivity gradients

On the left, parcels within the first three gradients that show significant (p_{bonf}<0.025) differences related to trait "introversion", orange indicating regions within the "frontoparietal control network", and violet indicating regions within the "ventral attention". Scatter plots depict the relationship between individual scores for "introversion" thought (x-axis) and average gradient score of all affected parcels (y-axis) within each gradient. Each datapoint is a participant. Both axes show standardized scores. Detailed results from individual parcels are reported in table 2. The right column shows Neurosynth decoding of ROI maps of affected parcels within each gradient, showing top ten positively correlated topic terms in red, and top ten negatively associated topic terms in blue.

Detailed internal cognition (Fig 5)

Relationships with patterns of detailed internal cognition were confined to the dorsal attention and visual networks. A region within the superior parietal lobule (DAN) had lower scores on the first gradient (more transmodal) and higher scores on the second gradient (less visual), indicating less similarity with visual regions whose ongoing experience was more “specific” and “internal”. Along the third gradient, higher “specific internal” thought scores were associated with greater separation between these regions and the default mode network. Finally, a parcel within the parahippocampal gyrus/ extrastriate (visual network) showed a broad spread along gradient one, with participants with higher “specific internal” thought scores falling on the transmodal/ DMN side and participants with lower scores (higher “surroundings”) closer to the visual system side.

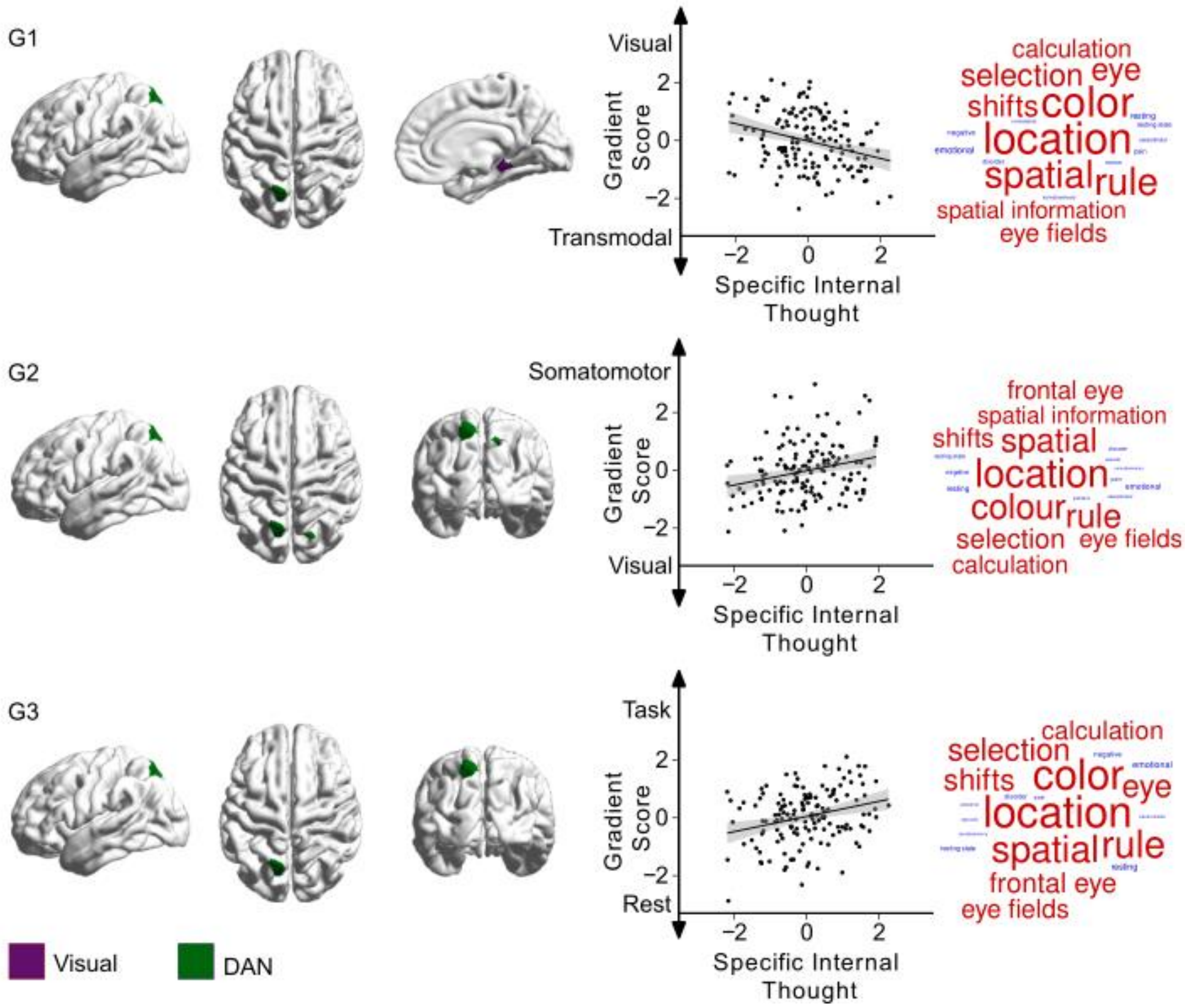

Figure 5. Relationship between specific internal thought and the first three connectivity gradients

On the left, parcels within the first three gradients that show significant differences (p_{bonf}<0.025) related to "specific internal" thought, green indicating regions within "dorsal attention network" (DAN), and purple indicating regions within the "visual network". Scatter plots depict the relationship between individual scores for "specific internal" thought (x-axis) and average gradient score of all affected parcels (y-axis) within each gradient. Each datapoint is a participant. Both axes show standardized scores. Detailed results from individual parcels are reported in table 1. The right column shows Neurosynth decoding of ROI maps of affected parcels within each gradient, showing top ten positively correlated topic terms in red, and top ten negatively associated topic terms in blue.

Table 2. Relationships between first three connectivity gradients and introversion and specific internal thought

IV	DV	Yeo Network	Parcel	$t_{(130)}$	p_{uncorr}	p_{bonf}
Introversion	G1	Control	OFC (R)	-4.2214	0.00002	0.0012
	G2	VAN	A Ins (L)	3.7888	0.00012	
			A Ins (R)	4.3110	0.00002	
			Fr Oper (R)	3.8081	0.00011	
			A Cing (R)	3.1879	0.00090	
		Control	P Cing (L)	4.0504	0.00004	
	G3	VAN	A Ins (L)	-3.9539	0.00006	
			A Ins (L)	-3.6784	0.00017	
			A Ins (R)	-4.2031	0.00002	
			Fr Oper (R)	-4.1767	0.00003	
			A Cing (R)	-3.9732	0.00006	
Specific Internal Thought	G1	Visual	PHC/ ExStr	-2.9105	0.00212	0.0028
		DAN	SPL (L)	-4.5433	0.00001	
	G2	DAN	SPL (L)	4.1217	0.00003	
		DAN	SPL (R)	3.3542	0.00052	
	G3	DAN	SPL (L)	4.4548	0.00001	

IV = Independent Variable, **DV** = Dependent Variable, **G** = Gradient, **VAN** = Ventral Attention Network, **DAN** = Dorsal Attention Network, **OFC** = Orbitofrontal Cortex, **A** = Anterior, **P** = Posterior, **Fr** = Frontal, **Ins** = Insula, **L**= Left, **R**= Right, **Oper** = Operculum, **Cing** = Cingulate Cortex, **PHC** = Parahippocampal Cortex, **ExStr** = Extrastriate cortex, **SPL** = Superior Parietal Lobule. Results reported in the table are from univariate (single-gradient) follow-up tests for parcels showing a significant effect for each IV at the multivariate (3-gradient) level. Univariate tests are Bonferroni corrected for the total number of parcels (all 3 gradients) where tests were performed (21 parcels for Introversion, 9 for Specific Internal Thought).

Discussion

Our study investigates whether an emerging "tri-partite" perspective from contemporary views of ongoing conscious thought can provide a framework that can account for the relationship between dispositional traits, ongoing thought, and individual differences in large scale patterns of neural connectivity at rest. This tri-partite network account emphasises the roles of regions embedded within three large scale networks as important for ongoing experience: the ventral attention network, the dorsal attention network and the default mode network (Smallwood et al., 2021; Huang et al., 2021). We calculated macro-scale connectivity gradients from one hour of resting state fMRI for 144 participants. The variability of these gradients was then analysed as a function of self-reports of ongoing thought patterns (captured by the principal components of MDES) and personality traits (described by the principal components of a battery of personality and habit measures). Given the tendency of certain traits to be correlated with frequency of specific patterns of thought (e.g. depression level with intrusive and negative thought (Konu et al., 2021) we also looked for possible dependencies between trait and thought components through multivariate regression using traits as predictors.

Our analyses confirmed that both patterns of thought, and indices of traits, contribute to patterns of brain organisation in a manner that converges with the emerging tri-partite view of ongoing conscious thought. For example, it has been hypothesised that the ventral attention network (VAN) helps adjudicate between internal and external influences on ongoing thought (Smallwood et al., 2021, Huang et al., 2021) and we found that individuals who were high on dispositional "introversion" showed variation in anterior insula, overlying operculum and ACC: all regions making up part of the VAN. For more introverted people these regions showed greater alignment with somatomotor regions and less with visual cortex (gradient 2), and greater alignment with default mode network than the fronto parietal network (gradient 3). Notably, prior studies have found that regions of sensorimotor cortex are linked to deliberate mind-wandering (Golchert et al., 2017) and individuals who tend to generate patterns of episodic social cognition during periods of low task demands show greater temporal correlation between the VAN and sensori-motor cortex (Turnbull et al., 2019a). Introversion reflects a predisposition towards internal subjective states rather than external objects (Jung, 1995), and so our analysis also suggests that there may be an important relationship between sensorimotor cortex and the ventral attention network in patterns of internal thought.

Our study also highlighted associations between observed patterns of neural organisation at rest and patterns ongoing thought are also consistent with hypothesized tripartite view (Smallwood et al., 2021, Huang et al., 2021). For example, we found a pattern of detailed thinking during wakeful rest that was correlated with stronger decoupling between a region within dorsal parietal cortex from the visual network (as indexed by changes in both gradients 1 and 2), and greater separation from the default mode network (gradient 3). This region overlaps with a region within the DAN identified by (Turnbull et al., 2019b) in which brain activity was reduced during self-generated thoughts relative to external task focus, suggesting an important role for the DAN in external facing attention. Furthermore, using a technique known as "echoes" analysis (Leech et al., 2012), Turnbull and colleagues established that individuals who engaged in self-generated thought during situations of low external demand, at rest showed greater separation between the dorsal attention network and lateral regions of the default mode network in a region of the dLPFC, also a member of the VAN. Together, therefore, the convergence between the current analysis and perspectives from research on conscious experience highlight a high degree of overlap in both the regions identified and the hypothesised functions. Our observations are important, therefore, because they help establish that, with the appropriate methodology (McKeown et al., 2020; Finn, 2021; Gonzalez-Castillo et al., 2021) neural accounts of conscious experience (Smallwood et al., 2021; Huang et al., 2021) provide an important valuable way to make sense of brain-cognition links observed at rest.

Second, our data provides evidence for the "decoupling" hypothesis of self-generated experience (Smallwood et al., 2013). This perspective emerged from observations that cortical processing of external inputs is reduced when individuals focus on internal self-generated thought (Smallwood et al., 2008; Kam et al., 2011; Baird et al., 2014), and assumes that this reduced processing of external input allows an internal train of thought to persist in a more detailed manner (p.524,Smallwood, 2013 (Smallwood, 2013b)). Our data is consistent with this view since both personality traits linked to internal focus ("introversion"), and patterns of detail experience that are not directed externally ("specific internal thought"), are linked to reductions in the similarity between neural activity in regions linked to attention and cognition, with regions of visual cortex. In this way our study provides novel insight into how the macro-scale functional patterns across the cortex support the emergence of detailed patterns of internal experience. Critically, in our study there was no external task from which thinking needed to be decoupled from, ruling out accounts of this process as a "lapse" in the normal upregulation of task relevant material needed for task completion (for discussion see Franklin et al., 2013, Smallwood 2013ab).

Although our study establishes how contemporary work on conscious experience can help understand patterns of brain organisation observed at rest and highlights how these approaches can be leveraged to understand the neural correlates of both an individuals' traits, and their thoughts, there are nonetheless important questions that our study leaves open. For example, contemporary work on ongoing conscious thought highlights time and context as key variables necessary for understanding the neural correlates of different features of thinking. Since the aim of our study was to focus on the brain at rest, interpretations of our results should bear in mind that under different task conditions, neural correlates between thinking, personality and neural activity may be different. For example, prior studies have established that posterior elements of the default mode network can become integrated into task positive systems (Krieger-Redwood et al., 2016; Vatansever et al., 2017) and under demanding task conditions the default mode network is linked to patterns of task focused cognition (Sormaz et al., 2018). Similarly, our analysis focused on 'static' indices of neural activity rather than dynamic measures. We chose to focus on static indices of neural activity because our prior studies have shown that brain-behaviour correlations can be relatively stable over time (Wang et al., 2020), and as we establish in our study these patterns show reasonable stability across a one hour session. Furthermore, our study, particularly with respect to the findings relating to DAN, map closely onto studies that use experience sampling to identify momentary correlations between neural activity and experience (Turnbull et al., 2019b, 2019a, 2020). Nonetheless, there are likely to be important features of ongoing experience that our analysis of static brain organisation cannot capture, and so we suggest that future work should explore dynamic changes in neural data and their links to cognition (Kucyi, 2018). It is worth noting that mapping momentary changes between in ongoing experience and neural activity will likely depend on a data set tailored to this question, in particular in which (i) experience sampling measures are collected more frequently as well as (ii) methodological advances that allow patterns of activity to be mapped without using temporal correlation. In addition, our analysis of the trait and thought data alone revealed that "neuroticism" was related to high negative and episodic thoughts, however, we did not find any other significant relationships among traits and thought patterns. In the current data, neuroticism was the most prominent out of all five traits included in the analysis, accounting for 50% of the total variance explained by them. It is therefore possible that correlations with other trait patterns may emerge with data sets with larger sample sizes and that measure thinking across multiple contexts.

Author Contributions

Jonathan Smallwood, and Samyogita Hardikar conceived of this study. Bronte Mckeown, Daniel Margulies, H. Lina Schaare, Reinder Vos de Wael, Mark Lauckner contributed analysis tools, and Samyogita Hardikar performed the analysis. Samyogita Hardikar and Jonathan Smallwood wrote the main manuscript text and Samyogita Hardikar prepared the figures. Boris Bernhardt, Daniel Margulies, Sofie L Valk, Mark Lauckner, Adam Turnbull, Ting Xu, and Arno Villringer provided help with the conceptual and methodological framework for this study, as well as feedback on the manuscript. All authors reviewed the final manuscript.

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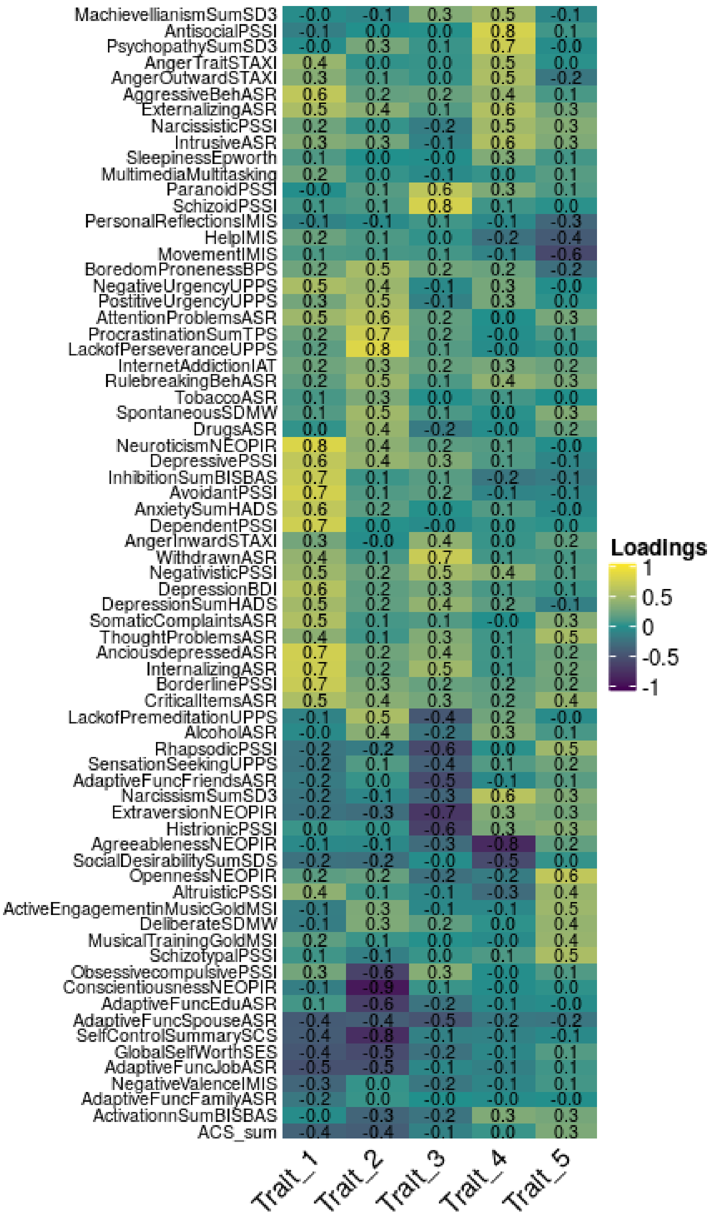
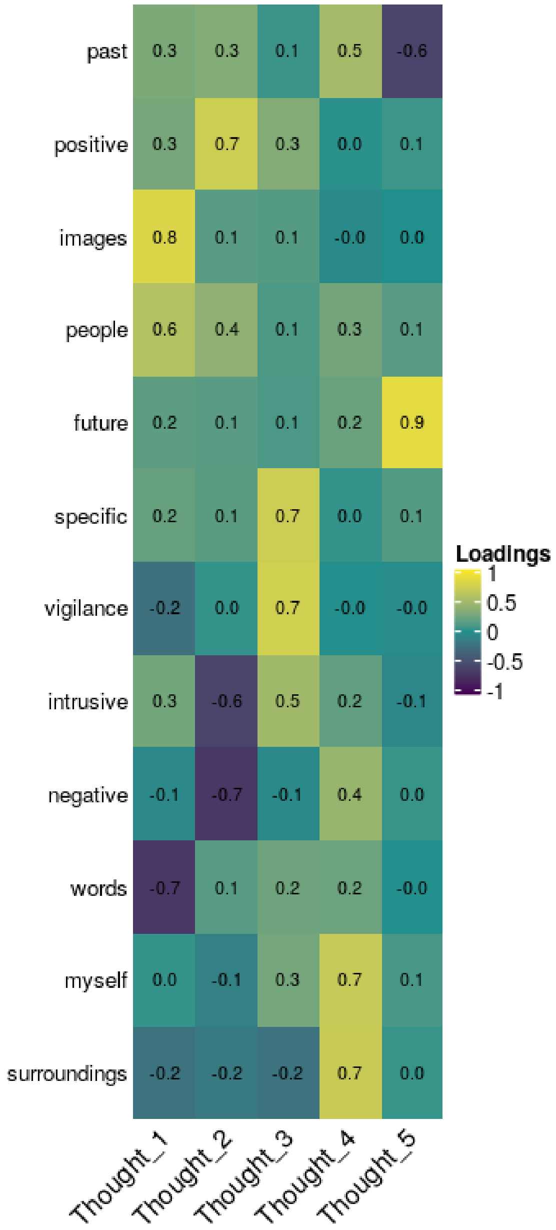
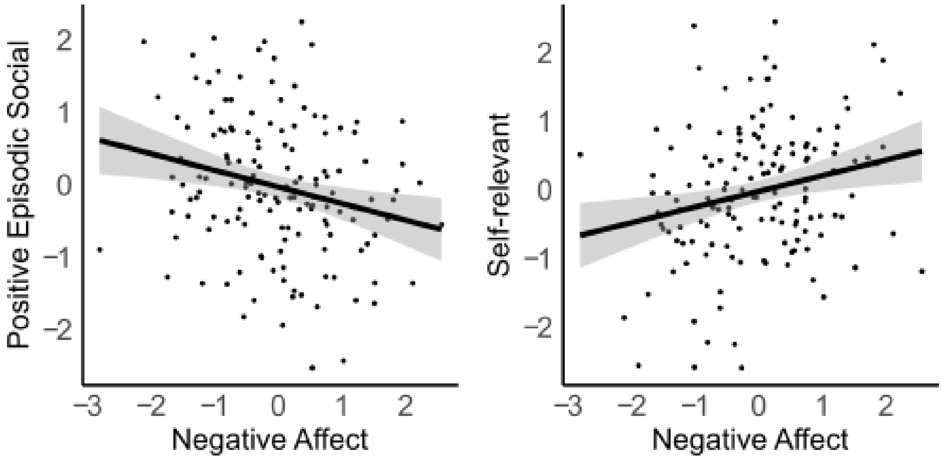
Supplementary figures



Supp. figure 1. Heatmap showing variable component loadings for the first 5 principal components derived from trait questionnaires



Supp. figure 2. Heatmap showing variable component loadings for the first 5 principal components derived from MDES



Supp. figure 3. Scatter-plots showing the relationship between trait "Negative affect", and "Positive Episodic Social" and "Self-relevant" thought.