

1 Macro-scale patterns in functional connectivity associated with 2 ongoing thought patterns and dispositional traits

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29

30 Abstract

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

52

53 Introduction

54 Macro-scale patterns of brain activity at rest have the potential for elucidating the organisation
55 of neural function, different types of psychiatric conditions (Cao et al., 2018; Koban et al.,
56 2021), developmental changes including those during adolescence and old age (Dosenbach
57 et al., 2010; Cui et al., 2020; Gratton et al., 2020; Wen et al., 2020), neurological disorders
58 (Zhang et al., 2021) and are important for revealing the neural basis behind the landscape of
59 self-generated experiences (Karapanagiotidis et al., 2019; Mckeown et al., 2020; Kucyi et al.,
60 2021). However, compared to controlled experimental conditions, interpreting neural activity
61 recorded during resting-state functional magnetic resonance imaging (rs-fMRI) is challenging,
62 partly because both trait-level aspects of the individual, and, the inherently complex and
63 dynamic nature of ongoing experience at rest are both contributory factors to the observed
64 brain activity (Smallwood et al., 2021b). It has recently been suggested that the meaning of
65 different patterns of neural activity can be usefully constrained by pairing imaging data at rest
66 with additional measures (Finn, 2021), for example by accounting for the patterns of thoughts
67 individuals experience at rest (Karapanagiotidis et al., 2020, 2021; Mckeown et al., 2020;
68 Gonzalez-Castillo et al., 2021; Kucyi et al., 2021), trait variation in how people think during
69 tasks (Smallwood et al., 2016) or features of their personality (Hsu et al., 2018). While this
70 methodological perspective is invaluable, we currently lack a theoretical framework within
71 which to understand the brain-cognition relationships that these observations will establish.
72 To address this gap in the literature, our study explores whether contemporary theories of the
73 neural basis of ongoing conscious thought can provide a framework within which to interpret
74 associations between macro-scale patterns of neural activity observed at rest, and measures
75 of traits and self-reports of ongoing experience.

76

77 Emerging views of how the brain supports patterns of ongoing conscious thought highlight
78 interactions between three large scale networks (Menon, 2011; Huang et al., 2021; Smallwood
79 et al., 2021b): the ventral attention network (VAN), the dorsal attention network (DAN) and the

80 default mode network (DMN)[⊕]. Traditionally, it was argued that the DMN was thought to have
81 an antagonistic relationship with systems linked to external processing (Fox et al., 2005).
82 However, according to the ‘tri-partite’ network accounts the relationship between the DMN and
83 other brain systems is more nuanced. From this perspective key hubs of the ventral attention
84 network, such as the anterior insula and dorso-lateral prefrontal cortex, help gate access to
85 conscious experience regardless of the focus of attention. This is hypothesised to occur
86 because the VAN influences interactions between the DAN, which is more important for
87 external mental content (Corbetta and Shulman, 2002), and the DMN which is important when
88 states (including tasks) rely more on internal representations (Smallwood et al., 2021a). For
89 example, Huang and colleagues (Huang et al., 2021) established that activity levels in the
90 anterior insula determine whether stimuli presented at perceptual threshold are consciously
91 perceived, and this gating of external input emerged as a consequence of changes in the
92 normal interactions between the DAN and DMN. They also found that disruptions to activity in
93 the insula through anaesthesia resulted in reductions in self-generated mental imagery.
94 Coming from a different perspective, Turnbull and colleagues (Turnbull et al., 2019b) used
95 experience sampling during task performance to link patterns of neural activity to different
96 features of ongoing thought. For example, they found activity in the dorsolateral prefrontal
97 cortex (a member of the VAN according to a parcellation by Yeo, Krienen and colleagues,
98 (Yeo et al., 2011) was correlated with apparently contradictory patterns of ongoing thought –
99 (i) self-generated episodic thoughts during periods of low demands, and (ii) patterns of detailed
100 task focus when individuals were engaged in demanding external task. In the same study,
101 however, neural activity within regions of the dorsal parietal cortex within the DAN, was
102 exclusively reduced when participants engaged in self-generated thinking, highlighting a
103 parallel neglect of external input seen by Huang and colleagues. Finally, in a second study,
104 Turnbull and colleagues found that at rest, trait variance in the ability to focus on self-
105 generated experience in laboratory situations with lower task demands is associated with

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

106 decoupling of signals arising from the DAN and DMN (Turnbull et al., 2019a). Summarising
107 this emerging evidence, studies focused on understanding ongoing thought patterns from
108 different perspectives converge on the view that regions of the VAN may be important for
109 gating conscious access to different types of content by biasing interactions between the DAN
110 and the DMN (Huang et al., 2021; Smallwood et al., 2021b).

111

112 Our current study explored whether this “tri-partite network” view of ongoing conscious thought
113 derived from studies focused on understanding conscious experience, provides a useful
114 organising framework for understanding the relation between observed brain activity at rest
115 and patterns of cognition/ personality traits. Such analysis is important because at rest there
116 are multiple features of brain activity that can be identified via complex analyses that include
117 regions that show patterns of coactivation (which are traditionally viewed as forming a
118 cohesive network, (Biswal et al., 1995) as well as patterns of anti-correlation with other regions
119 (e.g. Fox et al., 2005). However, it is unclear which of these relationships reflect aspects of
120 cognition or behaviour or are in fact aspects of the functional organisation of the cortex (Fox
121 and Raichle, 2007). Consequently, our study builds on foundational work (e.g.
122 Vanhaudenhuyse et al., 2011) in order to better understand which aspects of neural function
123 observed at rest are mostly likely linked to cognition and behaviour. With this aim in mind, we
124 examined links between macro-scale neural activation and both (i) trait descriptions of
125 individuals and (ii) patterns of ongoing thought. Our sample was a cohort of 144 participants
126 who underwent a one-hour resting-state scan. Across this one-hour period, participants were
127 interrupted on four occasions to answer a set of questions about their experiences at rest
128 using multidimensional experience sampling (MDES), similar to a number of prior
129 neuroimaging studies (Smallwood et al., 2016; Poerio et al., 2017; Wang et al., 2018). During
130 a different session, the same participants also completed a battery of measures assessing
131 features of their personality (such as the Big five (Costa and McCrae, 2008)) as well as
132 subclinical/ psychiatric traits such as trait anxiety and depression (Zigmond and Snaith, 1983).
133 Since our research question depends on understanding the hypothesised relationship

134 between large scale networks (VAN, DMN and DAN), we used the BrainSpace toolbox (Vos
135 de Wael et al., 2020) to provide whole brain low dimensional representations of functional
136 brain organisation, generating maps which represent the similarities and differences in the
137 activity within different systems. We used R version 4.2.0 (R Core Team, 2021) to produce
138 low dimensional representations of both traits and thoughts using principal component
139 analysis (PCA). Using these two sets of data, we performed multiple regression to identify how
140 brain network organisation varies with traits and states. In these analyses, the low dimensional
141 representations of brain organisation were the dependent measures, and the components of
142 traits and states were explanatory variables.

143

144 **Methods**

145 **Data**

146 The dataset used here is part of the MPI-Leipzig Mind-Brain-Body (MPILMBB) database
147 (Mendes et al., 2019). The complete dataset consists of a battery of self-reported personality
148 measures, measures of spontaneous thought, task data, and structural and resting-state
149 functional MRI from participants between 20 and 75 years of age. Data were collected over a
150 period of five days, with the MRI sessions always falling on day 3. The questionnaires were
151 completed by participants before and after this day, using Limesurvey
152 (<https://www.limesurvey.org>; version 2.00+) at their own convenience and using pen-and-
153 paper on-site. A detailed description of the participants, measures, and data acquisition
154 protocol has been previously published along with the dataset (Mendes et al., 2019).

155

156 **Participants**

157 We limited our investigation to personality and thought self-reports, and rs-fMRI from
158 participants under 50 years of age, who had complete data from at least three resting-state

159 scans. The resulting sample included 144 participants (74 men, mean age= 26.77 years, SD=
160 4.03; 70 women, mean age = 26.93 years, SD = 5.55).

161

162 Resting state fMRI with Multidimensional Experience Sampling (MDES)

163 The current sample includes one hour of fully pre-processed rs-fMRI data from 144
164 participants (four scans from 135 participants, and three scans from nine participants whose
165 data were missing or incomplete). The rs-fMRI was performed in four adjacent 15-minute
166 sessions each immediately followed by MDES which retrospectively measured various
167 dimensions of spontaneous thought during the scan. Images were acquired in axial orientation
168 using T2*-weighted gradient-echo echo planar imaging (GE-EPI) sensitive to blood oxygen
169 level-dependent (BOLD) contrast. Sequences were identical across the four runs, except for
170 alternating slice orientation and phase-encoding direction, to vary the spatial distribution of
171 distortions and signal loss. Motion correction parameters were derived by rigid-body
172 realignment of the time-series to the first (after discarding the first five volumes) volume with
173 FSL MCFLIRT (Jenkinson et al., 2002). Parameters for distortion correction were calculated
174 by rigidly registering a temporal mean image of this time series to the fieldmap magnitude
175 image using FSL FLIRT (Jenkinson and Smith, 2001) which was then unwarped using FSL
176 FUGUE (Jenkinson et al., 2012). Transformation parameters were derived by coregistering
177 the unwarped temporal mean to the subject's structural scan using FreeSurfer's boundary-
178 based registration algorithm (Greve and Fischl, 2009). All three spatial transformations were
179 then combined and applied to each volume of the original time series in a single interpolation
180 step. The time series was residualised against the six motion parameters, their first
181 derivatives, "outliers" identified by Nipype's rapidart algorithm
182 (<https://nipype.readthedocs.io/en/latest/interfaces/> A CompCor (Behzadi et al., 2007)
183 approach was implemented to remove physiological noise from the residual time-series- which
184 included first six principal components from all the voxels identified as white-matter
185 cerebrospinal fluid. The denoised time series were temporally filtered to a frequency range

186 between 0.01 and 0.1 Hz using FSL, mean centered and variance normalized using Nitime
187 (Rokem et al., 2009). Imaging and pre-processing protocols are described in detail in Mendes
188 et al (Mendes et al., 2019).

189

190 The MDES battery included 12 statements (Table 2) which participants rated on a visual
191 analog scale with 5% response increments that go from 0% = “describes my thoughts not at
192 all” to 100% = “describes my thoughts completely”. The current analysis sample includes
193 MDES data for all available instances of rs-fMRI scans for each participant.

194

Table 1. Multidimensional Experience Sampling (MDES) Statements

Dimension	Statement
Positive	“My thoughts were positive”
Negative	“My thoughts were negative.”
Future	“I thought about future events.”
Past	“I thought about past events.”
Myself	“I thought about myself.”
People	“I thought about other people.”
Surroundings	“I thought about my present environment/ surrounding.”
Wakeful	“I was completely awake.”
Images	“My thoughts were in the form of images.”
Words	“My thoughts were in the form of words”
Specific	“My thoughts were more specific than vague”
Intrusive	“My thoughts were intrusive”

195

196 Personality measures

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

199

200 **Table 2. 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., 2013)
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)

201

202 **Analyses**

203 Dimension reduction for questionnaire and MDES data

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

207

208 71 scores from the personality questionnaires of 144 participants were included and missing
209 data (3.15% of including all variables) were imputed by the variable mean. PCA was performed
210 on this matrix and five "trait" components (henceforth referred to as "traits") were selected on
211 the basis of eigenvalues >1 , using the Kaiser-Guttman criterion (Jolliffe, 2002) and their
212 congruence with the previously well-established "Big Five" personality traits (Digman, 1990;
213 Cobb-Clark and Schurer, 2012). For the MDES data, separate instances of responding for
214 each participant were concatenated, resulting in a matrix with 576 observations of 12
215 variables. PCA was performed on this matrix, and five "thought" components (henceforth
216 referred to as "thought patterns") were selected on the basis of eigenvalues >1 . Varimax
217 rotation was applied to both solutions to optimize the distinctiveness of each component. The
218 five thought pattern scores were then averaged across the four scans, resulting in one score

219 for each thought pattern for each participant, describing their location on a particular thought
220 dimension.

221

222 Dimension reduction for whole-brain functional connectivity

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

229

230 In order to summarize whole brain connectivity in a low-dimensional space, we performed
231 gradient analysis using the BrainSpace toolbox (Vos de Wael et al., 2020). 10 macro-scale
232 gradients were calculated for the group (Figure 2). First, we applied fisher's z transform to the
233 group matrix, building an affinity matrix (kernel= normalized angle, sparsity= 0.9) and then
234 decomposed it using PCA. We chose the PCA approach for gradient calculation, as Hong and
235 colleagues (Hong et al., 2020) have shown that compared to non-linear decomposition
236 methods, PCA provides better reliability and higher phenotypic predictive value for
237 connectivity gradients. For ease of interpretation and comparability, group gradients were
238 aligned to a subsample of the HCP dataset (Van Essen et al., 2013) included in BrainSpace.
239 Finally, following Mckeown et al. (Mckeown et al., 2020) 10 gradients were calculated in order
240 to maximize the gradient fit for all individuals during alignment. Individual gradients were
241 calculated for each participant, aligned to the group-level gradients, resulting in a 400x10
242 matrix for each participant. 10 gradients were calculated to facilitate alignment across
243 individuals irrespective of differences in rank order of individual gradients (to control for the
244 possibility, for example, that the pattern summarised by group-level Gradient 2 is Gradient 4
245 for some participants). Subsequent regression analyses were limited to the first three group-

246 aligned gradients, which have been relatively well-characterized in previous work (Margulies
247 et al., 2016; Mckeown et al., 2020; Turnbull et al., 2020b). To visualize the functional axis
248 captured by each gradient, we performed Neurosynth (Yarkoni et al., 2011) decoding on the
249 group gradient maps (Figure 2). Further, we calculated the average gradient score for all
250 parcels within each of the seven connectivity networks described by Yeo and colleagues (Yeo
251 et al., 2011) (Figure 2).

252

253 Stability of thoughts-patterns and gradients

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

265

266 Multiple Multivariate Regression

267 To investigate the relationship between individual differences in traits, thoughts, and macro-
268 scale cortical gradients, we used multiple multivariate regression as implemented in the
269 MATLAB SurfStat Toolbox (Worsley et al., 2009) [<http://www.math.mcgill.ca/keith/surfstat/>].
270 400 separate linear models were estimated for 400 parcels, with the gradient scores from the
271 first three gradients as the dependent variables, and with five trait scores (Figure 1A) and five
272 thought scores (Figure 1B), as well as nuisance variables age, motion, and gender included

273 as independent variables. The resulting significant effects from 400 parcels were corrected for
274 False Discovery Rate (FDR, $q < .05$) (Storey, 2003) at the multivariate (three gradients) level.
275 In order to test which gradient score was affected, follow-up univariate analyses were
276 performed on the resulting parcels for each gradient separately, and effects were further
277 Bonferroni corrected ($p_{\text{bonf}} < .025$) for the total number of comparisons performed for all parcels
278 (including the analyses of all three gradients) for each variable. Additionally, to see how the
279 trait components related to the thought components, we performed multiple multivariate
280 regression with the thoughts as dependent variables and traits as independent variables.

281

282 Results

283 Traits and thought patterns

284 Application of PCA to the battery of personality questionnaires resulted in five “traits” (Figure
285 1 A, Supplementary Figure 1) with eigenvalues > 1 , explaining 48.4% of the variance. The five
286 trait components, independent of the direction of loadings, largely map onto the “big five”
287 personality factors: neuroticism, conscientiousness (positive loading on “procrastination” in
288 our PCA result), extraversion (positive loading on “introversion” in our PCA result),
289 agreeableness (positive loading on anti-social in our results) and openness to experience,
290 respectively. Application of PCA to the MDES questions revealed five “thought patterns”
291 (Figure 1B, Supplementary Figure 2) with eigenvalues > 1 , explaining 65.4% of the variance.
292 Based on the most heavily loaded dimensions within each pattern, we named these: “modality”
293 (image vs words), “positive episodic social”, “specific internal”, “self-relevant” and
294 “prospective”.

295

296 Intraclass correlation – thoughts

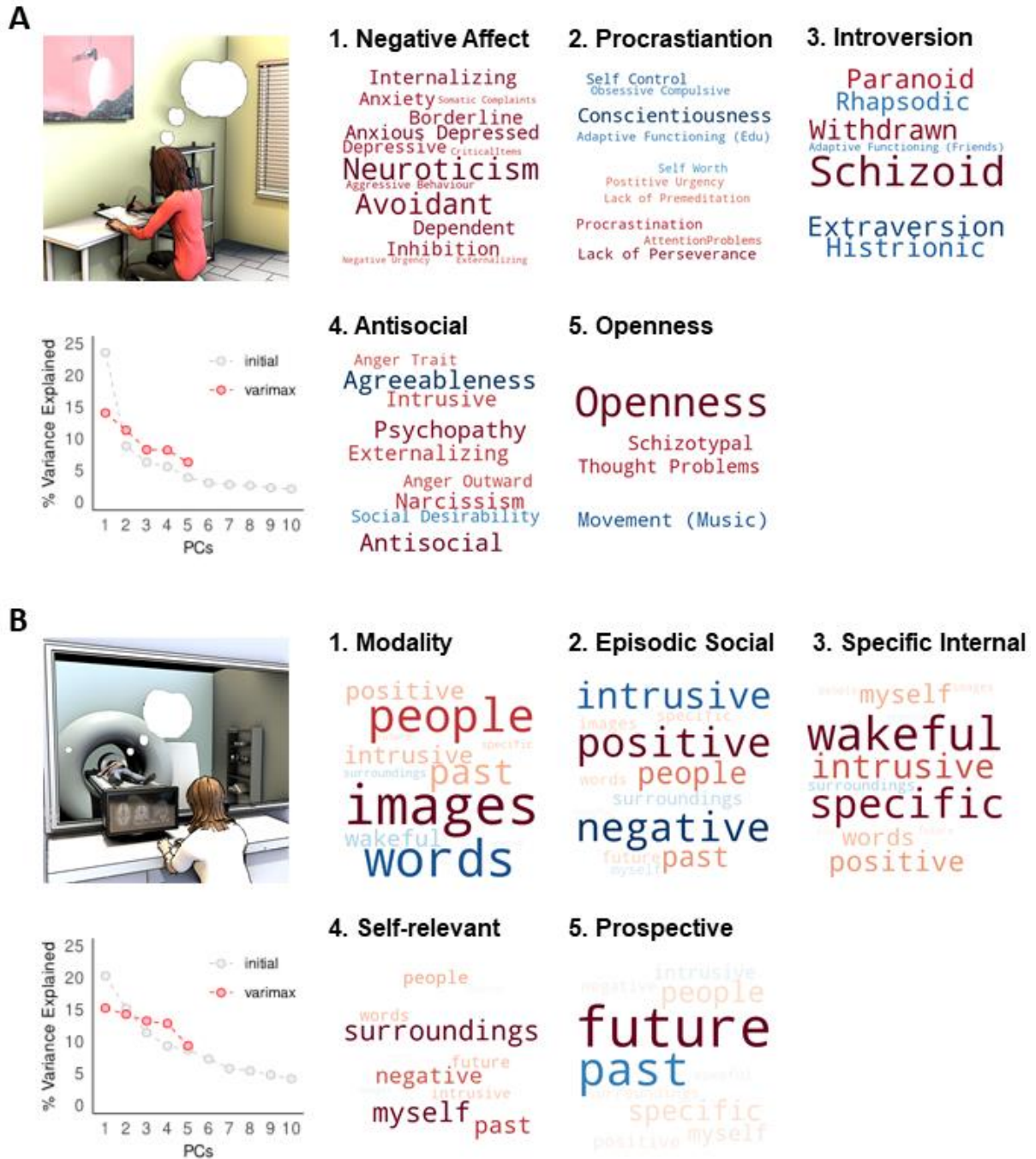
297 Our first analysis established the reliability of thought components across the one hour of
298 scanning. The five thought patterns showed low to moderate agreement between individual

299 scores from single sessions (modality = 0.5856, positive episodic-social= 0.4531, specific
300 internal= 0.5226, self-relevant = 0.5832, prospective= 0.3118), indicating a degree of
301 variability between sessions. The average of all scores had high ICCs for the first four
302 components (modality = 0.8497, positive episodic social = 0.7783, specific internal = 0.8141,
303 self-relevant = 0.8484, prospective = 0.6444). The average scores from 4 sessions were used
304 as regressors in subsequent analyses.

305

306 Next, we examined the relationship between the low dimensional representations of both
307 personality and thoughts. Multiple multivariate regression using traits as predictor variables of
308 thought patterns established that “negative affect” had a significant effect on thoughts ($F_{(5,134)} =$
309 3.88, $p = 0.003$, partial $\eta^2 = 0.127$). Univariate follow-up showed that a high score on trait
310 neuroticism was significantly associated with less “positive episodic social” thought (pattern 2;
311 $\beta = -0.229$, 95% CI = [-0.389 -0.07], $p = 0.005$, partial $\eta^2 = 0.055$) as well as greater “self-
312 relevant” thought (pattern 4; $\beta = 0.229$, 95% CI = [0.066 0.391], $p = 0.006$, partial $\eta^2 = 0.053$),
313 (Supplementary Fig. 4).

314



315

316

317 **Figure 1. Principal components of traits and thoughts**

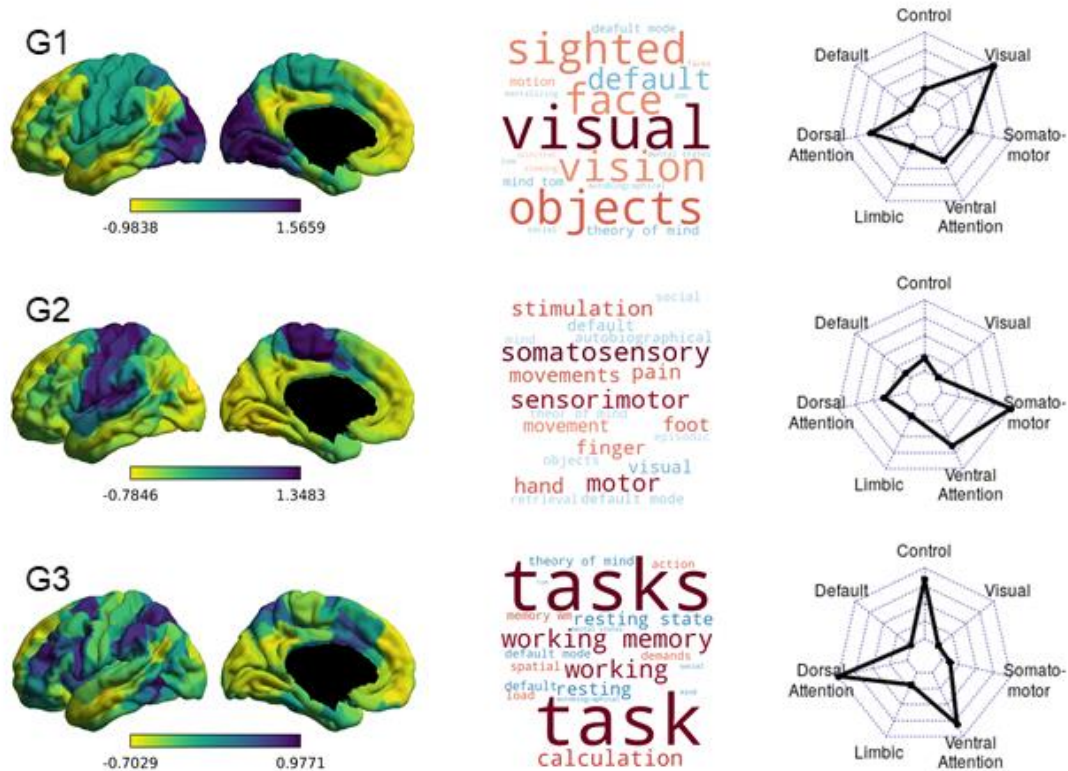
318 **A)** First five trait components derived from PCA after varimax rotation are represented as
 319 word-clouds with negative loadings shown in cold colours and positive loadings in warm
 320 colours; the relative loading of each variable within a component is represented by the relative
 321 font size (See Supp Figures 1 and 2 for numerical loading values). In the bottom left panel,
 322 scree-plot showing the percentage of trait variance explained by the each of the first 10

323 components in grey, and the first five components after varimax rotation in red. **B)** Results of
324 the application of PCA to the MDES data, depicted in the same way.

325

326 **Macro-scale cortical gradients**

327 The first three group level gradients are shown in Figure 2 along with their Neurosynth meta-
328 analytic associations and relationships to the Yeo-networks (Yeo et al., 2011) (7-network
329 solution). The first gradient (G1) differentiates between visual regions at one end and DMN at
330 the other. The second gradient (G2) describes the dissociation between somatomotor and
331 visual cortices. The third gradient (G3) captures the segregation between different transmodal
332 systems (the default mode network versus the fronto-parietal system). The three gradients are
333 largely similar to the ones reported by Margulies et al. (Margulies et al., 2016) and subsequent
334 literature (Hong et al., 2019; Paquola et al., 2019; Bethlehem et al., 2020; Mckeown et al.,
335 2020; Turnbull et al., 2020b). Due to the difference in the decomposition provided by PCA vs.
336 DM approach, the endpoints of G1 are different from those first reported by Margulies et al
337 (Margulies et al., 2016) in that one end is anchored by the visual network alone, as opposed
338 to visual and somatomotor, while in G2, the somatomotor network is separated from both the
339 visual and default mode networks, as opposed to the visual network alone in the (Margulies
340 et al., 2016) study. However, like those reported by Margulies and colleagues, the first two
341 gradients together describe network-level connectivity space anchored at three ends by the
342 visual, somatomotor and default mode network, respectively (Figure 3). Stability of results
343 irrespective of the decomposition approach is shown in supplementary Figure 4. Single
344 gradients tended to be stable over the 4 sessions, with a discriminability index of 0.964 for
345 Gradient 1, 0.918 for Gradient 2, and 0.983 for Gradient 3 over four adjacent scans from 135
346 participants. Discriminability indices are similar to those previously reported by (Hong et al.,
347 2020).

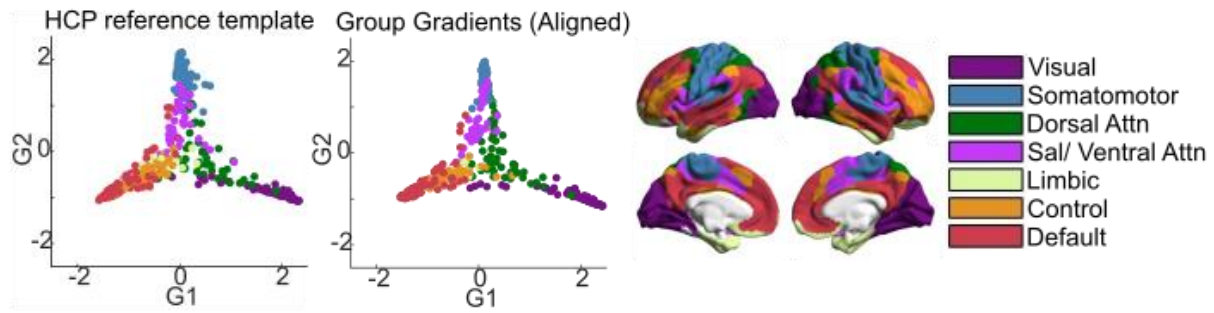


348

349 **Figure 2. Group-level gradients of functional connectivity**

350 On the left are the first three group-averaged gradients, represented in left lateral and medial
351 views. Regions with similar whole-brain connectivity profiles are shown in similar colours, with
352 yellow and purple regions indicating most dissimilar connectivity patterns. Loading ranges and
353 directions are arbitrary. In the middle, word clouds representing the top 10 positively (warm
354 colours) and negatively correlated (cold colours) Neurosynth decoding topic terms for each
355 gradient map. The relative strength of correlation is represented by the relative font size. On
356 the right, radar-plots showing the Yeo-network profile of each group-level gradient depicted in
357 the left column. Each radar-plot shows the mean gradient loadings for all parcels within the
358 seven Yeo networks.

359



360

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

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

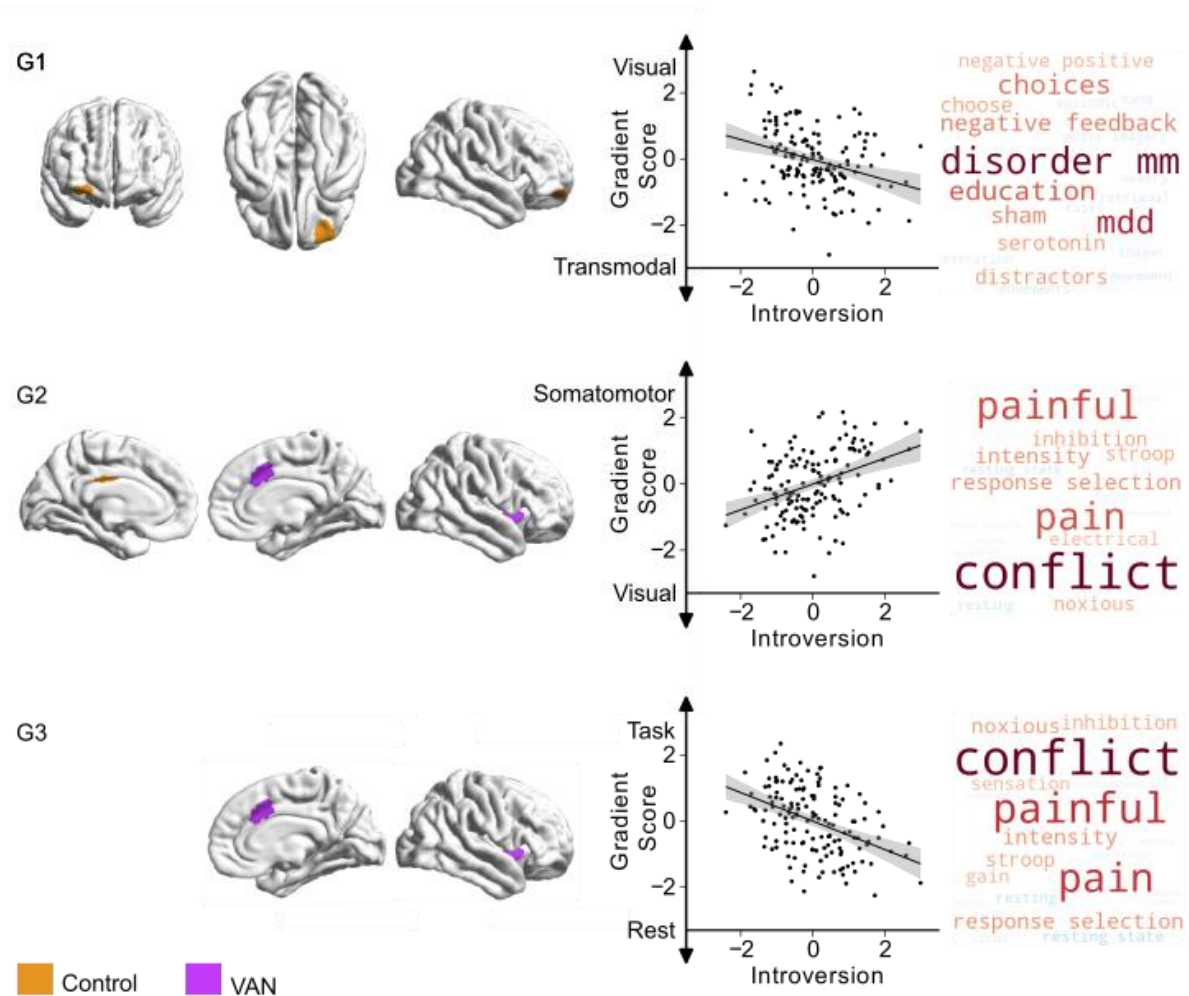
367

368 **Relationship between state- trait variability and cortical gradients**

369 Having established low dimensional representations of thought, personality, and brain
370 organisation, we next examined associations between different types of personality and
371 ongoing thought experienced during the scan and our metrics of functional brain organisation.
372 To this end, we performed a multiple multivariate regression with thoughts, traits, and nuisance
373 variables (motion, age and gender) as independent variables, with whole brain functional
374 organisation, as captured by the first three gradients, as dependent variables. In this analytic
375 approach relationships between cognition along one gradient but not along another help
376 identify which relationships between brain systems are mostly likely to relate to the feature of
377 cognition in question (i.e. each gradient acts as a control for the other). In these analyses
378 both trait “introversion” and a pattern describing “specific internal” thought showed significant
379 effects at the multivariate level. Results from the univariate follow-up of effects within each
380 gradient are shown in Figures 4 and 5, and Table 3.

381 Trait Introversion

382 Along the first gradient, a parcel within the right orbitofrontal cortex (within the executive
383 control network, shown in orange) showed more similarity with transmodal regions for
384 individuals high on introversion. Six parcels within the ventral attention network, including
385 anterior insula, operculum and cingulate cortex were closer to the somatomotor end along
386 gradient two (shown in purple). The same regions showed lower scores along the third
387 gradient in participants with higher introversion scores, indicating stronger integration with the
388 default mode network. A parcel within posterior cingulate cortex (control) was also more
389 segregated from the visual end of gradient two in participants with higher introversion scores.
390 Associations between trait “introversion” and brain-wide activity are shown in Figure 4.



391

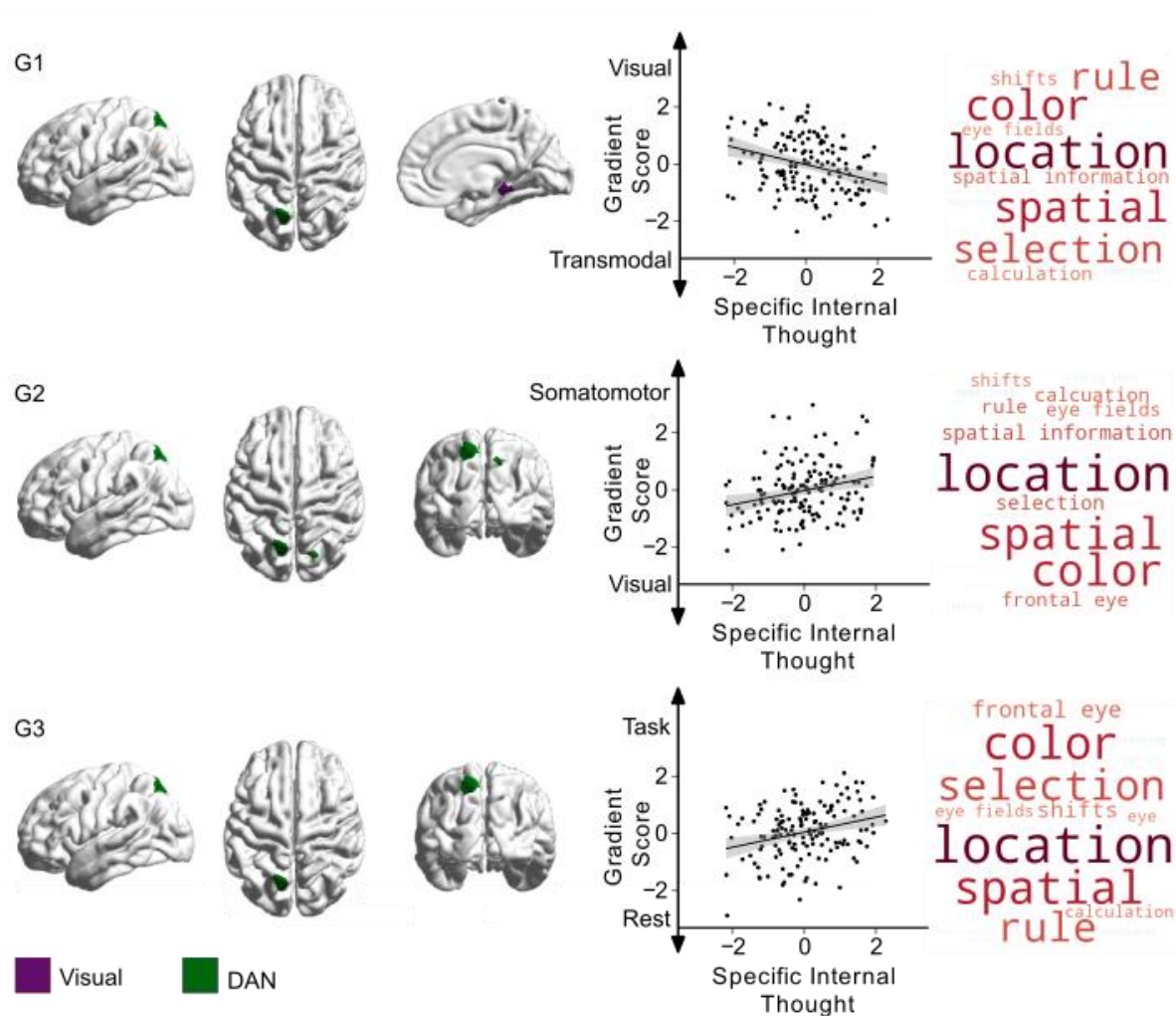
392 **Figure 4. Relationship between trait “Introversion” on the first three connectivity**
393 **gradients**

394 On the left, parcels within the first three gradients that show significant ($p_{\text{bonf}} < 0.025$)
395 differences related to trait “introversion”, orange indicating regions within the “frontoparietal
396 control network”, and violet indicating regions within the “ventral attention”. Scatter plots depict
397 the relationship between individual scores for “introversion” thought (x-axis) and average
398 gradient score of all affected parcels (y-axis) within each gradient. Each datapoint is a
399 participant. Both axes show standardized scores. Detailed results from individual parcels are
400 reported in Table 3. The right column shows Neurosynth decoding of ROI maps of affected
401 parcels within each gradient, showing top ten positively correlated topic terms in warm colours,
402 and top ten negatively associated topic terms in cold colours.

403

404 Specific internal cognition

405 Relationships with patterns of more specific internal cognition were confined to the dorsal
406 attention and visual networks. A region within the superior parietal lobule (DAN) had lower
407 scores on the first gradient (more transmodal) and higher scores on the second gradient (less
408 visual), indicating less similarity with visual regions whose ongoing experience was more
409 “specific” and “internal”. Along the third gradient, higher “specific internal” thought scores were
410 associated with greater separation between these regions and the default mode network.
411 Finally, a parcel within the parahippocampal gyrus/ extrastriate (visual network) showed a
412 broad spread along gradient one, with participants with higher “specific internal” thought
413 scores falling on the transmodal/ DMN side and participants with lower scores (higher
414 “surroundings”) closer to the visual system side. These findings are shown in Figure 5.



415

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

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

427 **Table 3. Relationships between first three connectivity gradients and introversion and**
 428 **specific internal thought**

IV	DV	Yeo Network	Parcel	t₍₁₃₀₎	η^2_{partial}	p_{uncorr}	p_{bonf}	
Introversion	G1	Control	OFC (R)	-4.2214	0.11	0.00002	<0.0012	
			A Ins (L)	3.7888	0.10	0.00012		
	G2	VAN	A Ins (R)	4.3110	0.12	0.00002		
			Fr Oper (R)	3.8081	0.10	0.00011		
			A Cing (R)	3.1879	0.06	0.00090		
			Control	P Cing (L)	4.0504	0.07	0.00004	
			G3	VAN	A Ins (L)	-3.9539	0.11	0.00006
					A Ins (L)	-3.6784	0.09	0.00017
					A Ins (R)	-4.2031	0.13	0.00002
					Fr Oper (R)	-4.1767	0.12	0.00003
					A Cing (R)	-3.9732	0.12	0.00006
			Specific	G1	Visual	PHC/ ExStr	-2.9105	0.05
	Internal		DAN	SPL (L)	-4.5433	0.12	0.00001	
	Thought	G2	DAN	SPL (L)	4.1217	0.09	0.00003	
SPL (R)				3.3542	0.09	0.00052		
G3		DAN	SPL (L)	4.4548	0.10	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).

429 Discussion

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

445

446 Our analyses confirmed that both patterns of thought, and indices of traits, contribute to
447 patterns of brain organisation in a manner that converges with the emerging tri-partite view of
448 ongoing conscious thought. For example, it has been hypothesised that the ventral attention
449 network (VAN) helps adjudicate between internal and external influences on ongoing thought
450 (Huang et al., 2021; Smallwood et al., 2021b) and we found that individuals who were high on
451 dispositional “introversion” showed variation in anterior insula, overlying operculum and ACC:
452 all regions making up part of the VAN. For more introverted people these regions showed
453 greater alignment with somatomotor regions and less with visual cortex (gradient 2), and
454 greater alignment with default mode network than the fronto-parietal network (gradient 3).
455 Notably, prior studies have found that regions of sensorimotor cortex are linked to deliberate

456 mind-wandering (Golchert et al., 2017) and individuals who tend to generate patterns of
457 episodic social cognition during periods of low task demands show greater temporal
458 correlation between the VAN and sensori-motor cortex (Turnbull et al., 2019a). Introversions
459 reflects a predisposition towards internal subjective states rather than external objects (Jung,
460 1995), and so our analysis adds to an emerging literature (Golchert et al., 2017; Turnbull et
461 al., 2019a) that suggests that there may be an important relationship between sensorimotor
462 cortex and the ventral attention network in patterns of internal self-generated thought.

463

464 Our study also highlighted that associations between observed patterns of neural organisation
465 at rest and patterns of ongoing thought are consistent with the hypothesized tripartite view
466 (Huang et al., 2021; Smallwood et al., 2021b). For example, we found a pattern of detailed
467 thinking during wakeful rest that was correlated with stronger decoupling between a region
468 within dorsal parietal cortex from the visual network (as indexed by changes in both gradients
469 1 and 2), and greater separation from the default mode network (gradient 3). This region
470 overlaps with a region within the DAN identified by (Turnbull et al., 2019b) in which brain
471 activity was reduced during self-generated thoughts relative to external task focus, suggesting
472 an important role for the DAN in external facing attention. Furthermore, using a technique
473 known as “echoes” analysis (see Leech et al., 2012), Turnbull and colleagues (Turnbull et al.,
474 2019b) established that individuals who engaged in self-generated thought during situations
475 of low external demand, at rest showed greater separation between the dorsal attention
476 network and lateral regions of the default mode network in a region of the dLPFC, also a
477 member of the VAN. Thus, our study confirms prior studies that highlight that greater
478 segregation between the DAN and the DMN in the capacity to engage in thoughts that are
479 less linked to the external environment. Together, the convergence between the current
480 analysis and perspectives from research on conscious experience highlight a high degree of
481 overlap in both the regions identified and the hypothesised functions. Our observations are
482 important, therefore, because they help establish that with the appropriate methodology
483 (Mckeown et al., 2020; Finn, 2021; Gonzalez-Castillo et al., 2021) neural accounts of

484 conscious experience (Huang et al., 2021; Smallwood et al., 2021b) provide an important
485 valuable way to make sense of brain-cognition links observed at rest. Second, our data
486 provides evidence for the “decoupling” hypothesis of self-generated experience (Smallwood,
487 2013a). This perspective emerged from observations that cortical processing of external
488 inputs is reduced when individuals focus on internal self-generated thought (Smallwood et al.,
489 2008; Kam et al., 2011; Baird et al., 2014), and assumes that this reduced processing of
490 external input allows an internal train of thought to persist in a more detailed manner
491 (p.524, Smallwood, 2013 Smallwood, 2013b)). Our data is consistent with this view since both
492 personality traits linked to internal focus (“introversion”), and patterns of detail experience that
493 are not directed externally (“specific internal thought”), are linked to reductions in the similarity
494 between neural activity in regions linked to attention and cognition, with regions of visual
495 cortex. In this way our study provides novel insight into how the macro-scale functional
496 patterns across the cortex support the emergence of detailed patterns of internal experience.
497 Critically, in our study there was no external task from which thinking needed to be decoupled
498 from, ruling out accounts of this process as a “lapse” in the normal upregulation of task relevant
499 material needed for task completion (for discussion see Franklin et al., 2013, Smallwood
500 2013ab).

501

502 Although our study establishes how contemporary work on conscious experience can help
503 understand patterns of brain organisation observed at rest and highlights how these
504 approaches can be leveraged to understand the neural correlates of both an individuals’ traits,
505 and their thoughts, there are nonetheless important questions that our study leaves open. For
506 example, contemporary work on ongoing conscious thought highlights time and context as
507 key variables necessary for understanding the neural correlates of different features of thinking
508 (Smallwood et al., 2021b). Since the aim of our study was to focus on the brain at rest,
509 interpretations of our results should bear in mind that under different task conditions, neural
510 correlates between thinking, personality and neural activity may be different. For example,
511 prior studies have established that posterior elements of the default mode network can

512 become integrated into task positive systems (Krieger-Redwood et al., 2016; Vatansever et
513 al., 2017) and under demanding task conditions the default mode network is linked to patterns
514 of task focused cognition (Sormaz et al., 2018). Similarly, our analysis focused on ‘static’
515 indices of neural activity rather than dynamic measures. We chose to focus on static indices
516 of neural activity because our prior studies have shown that brain-behaviour correlations can
517 be relatively stable over time (Wang et al., 2020), and as we establish in our study these
518 patterns show reasonable stability across a one hour session. Furthermore, our study,
519 particularly with respect to the findings relating to DAN, map closely onto studies that use
520 experience sampling to identify momentary correlations between neural activity and
521 experience (Turnbull et al., 2019b, 2019a, 2020b). Nonetheless, there are likely to be
522 important dynamic features of ongoing experience that our analysis of static brain
523 organisation cannot capture (Kucyi, 2018). Recent discussions in cognitive neuroscience
524 have highlighted the link between sample size and the reproducibility of brain-wide
525 associations with behavioural phenotypes (Marek et al., 2022; Spisak et al., 2023). Our
526 analysis of the trait and thought data alone revealed that “neuroticism” was related to high
527 negative and episodic thoughts, however, we did not find any other significant relationships
528 among traits and thought patterns. In the current data, neuroticism was the most prominent
529 out of all five traits included in the analysis, accounting for 29% of the total variance explained
530 by them. It is therefore likely that more extensive and robust correlations between thoughts
531 patterns and other traits, as well as thoughts, traits and macroscale connectivity patterns
532 would emerge with data sets with larger sample sizes. In the future it may also be important
533 to consider measures of traits that could have relationships to both neural activity and or
534 experience at rest (e.g. self-consciousness de Caso et al., 2017, or autistic tendencies,
535 Turnbull et al., 2020a). It is worth noting that mapping momentary changes between ongoing
536 experience and neural activity will likely depend on a data set tailored to this question, in
537 particular in which (i) experience sampling measures are collected more frequently as well as
538 (ii) methodological advances that allow patterns of activity to be mapped without using
539 temporal correlation. and that measure thinking across multiple contexts.

540 References

541

542 Achenbach TM, Rescorla LA (2003) *Manual for the ASEBA adult forms & profiles.*
543 Research Center for Children, Youth, & Families. University of Vermont, Burlington, VT,
544 USA.

545 Baird B, Smallwood J, Lutz A, Schooler JW (2014) The Decoupled Mind: Mind-wandering
546 Disrupts Cortical Phase-locking to Perceptual Events. *J Cogn Neurosci* 26:2596–2607.

547 Beck A, Steer R, Brown G (1993) Beck Depression Inventory-II (BDI-II). ... Beck Depress
548 Invent.

549 Behzadi Y, Restom K, Liao J, Liu TT (2007) A component based noise correction method
550 (CompCor) for BOLD and perfusion based fMRI. *Neuroimage* 37:90–101 Available at:
551 [/pmc/articles/PMC2214855/](https://pubmed.ncbi.nlm.nih.gov/16290344/) [Accessed July 5, 2021].

552 Bethlehem RAI, Paquola C, Seidlitz J, Ronan L, Bernhardt B, Consortium C-CCAN,
553 Tsvetanov KA (2020) Dispersion of functional gradients across the adult lifespan.
554 *Neuroimage* 222:117299 Available at:
555 <https://linkinghub.elsevier.com/retrieve/pii/S1053811920307850> [Accessed November
556 3, 2021].

557 Biswal B, Zerrin Yetkin F, Haughton VM, Hyde JS (1995) Functional connectivity in the
558 motor cortex of resting human brain using echo-planar mri. *Magn Reson Med* 34:537–
559 541 Available at: <https://onlinelibrary.wiley.com/doi/full/10.1002/mrm.1910340409>
560 [Accessed April 11, 2024].

561 Bridgeford EW, Wang S, Yang Z, Wang Z, Xu T, Craddock C, Dey J, Kiar G, Gray-Roncal
562 W, Colantuoni C, Douville C, Noble S, Priebe CE, Caffo B, Milham M, Zuo X-N,
563 Reproducibility C for R and, Vogelstein JT (2021) Eliminating accidental deviations to
564 minimize generalization error and maximize replicability: applications in connectomics
565 and genomics. *bioRxiv:802629* Available at:
566 <https://www.biorxiv.org/content/10.1101/802629v8> [Accessed September 24, 2021].

567 Cao H et al. (2018) Cerebello-thalamo-cortical hyperconnectivity as a state-independent
568 functional neural signature for psychosis prediction and characterization. *Nat Commun*
569 9 Available at: [/pmc/articles/PMC6155100/](https://pubmed.ncbi.nlm.nih.gov/30000000/) [Accessed March 22, 2022].

570 Carriere JSA, Seli P, Smilek D (2013) Wandering in both mind and body: Individual
571 differences in mind wandering and inattention predict fidgeting. *Can J Exp Psychol Can*
572 *Psychol expérimentale* 67:19–31 Available at:
573 <http://doi.apa.org/getdoi.cfm?doi=10.1037/a0031438> [Accessed April 4, 2019].

574 Carver CS, White TL (1994) Behavioral Inhibition , Behavioral Activation , and Affective
575 Responses to Impending Reward and Punishment : The BIS / BAS Scales. *J Pers Soc*
576 *Psychol* 67:319–333.

577 Cobb-Clark DA, Schurer S (2012) The stability of big-five personality traits. *Econ Lett*
578 115:11–15.

579 Corbetta M, Shulman GL (2002) Control of goal-directed and stimulus-driven attention in the
580 brain. *Nat Rev Neurosci* 3:201–215 Available at:
581 <https://pubmed.ncbi.nlm.nih.gov/11994752/> [Accessed March 21, 2022].

582 Costa PT, McCrae RR (2008) *The revised NEO personality inventory (NEO-PI-R).* SAGE
583 *Handb Personal Theory Assess Vol 2 - Personal Meas Test:179–198.*

584 Crowne DP, Marlowe D (1960) A new scale of social desirability independent of

- 585 psychopathology. *J Consult Psychol* 24:349–354.
- 586 Cui Z et al. (2020) Individual Variation in Functional Topography of Association Networks in
587 Youth. *Neuron* 106:340-353.e8.
- 588 de Caso I, Poerio G, Jefferies E, Smallwood J (2017) That's me in the spotlight: neural basis
589 of individual differences in self-consciousness. *Soc Cogn Affect Neurosci* 12:1384
590 Available at: [/pmc/articles/PMC35629813/](https://pubmed.ncbi.nlm.nih.gov/35629813/) [Accessed April 11, 2024].
- 591 Derryberry D, Reed MA (2002) Anxiety-related attentional biases and their regulation by
592 attentional control. *J Abnorm Psychol* 111:225–236 Available at: [/record/2002-12652-](https://pubmed.ncbi.nlm.nih.gov/12652002/)
593 002 [Accessed September 24, 2021].
- 594 Digman JM (1990) PERSONALITY STRUCTURE: EMERGENCE OF THE FIVE-FACTOR
595 MODEL. *Annu Rev Psychol* 41:417–457 Available at: www.annualreviews.org
596 [Accessed October 10, 2023].
- 597 Dosenbach NUF, Nardos B, Cohen AL, Fair DA, Power JD, Church JA, Nelson SM, Wig GS,
598 Vogel AC, Lessov-Schlaggar CN, Barnes KA, Dubis JW, Feczko E, Coalson RS, Pruett
599 JR, Barch DM, Petersen SE, Schlaggar BL (2010) Prediction of individual brain maturity
600 using fMRI. *Science* (80-) 329:1358–1361 Available at:
601 <https://www.science.org/doi/abs/10.1126/science.1194144> [Accessed March 21, 2022].
- 602 Farmer R, Sundberg ND (1986) Boredom proneness--the development and correlates of a
603 new scale. *J Pers Assess* 50:4–17 Available at:
604 <https://europepmc.org/article/MED/3723312> [Accessed September 24, 2021].
- 605 Finn ES (2021) Is it time to put rest to rest? *Trends Cogn Sci* Available at:
606 <https://linkinghub.elsevier.com/retrieve/pii/S1364661321002345> [Accessed October 14,
607 2021].
- 608 Floridou GA, Williamson VJ, Stewart L, Müllensiefen D (2015) The Involuntary Musical
609 Imagery Scale (IMIS). *Psychomusicology Music Mind, Brain* 25:28–36 Available at:
610 [/record/2015-22418-001](https://pubmed.ncbi.nlm.nih.gov/22418001/) [Accessed September 24, 2021].
- 611 Fox MD, Raichle ME (2007) Spontaneous fluctuations in brain activity observed with
612 functional magnetic resonance imaging. *Nat Rev Neurosci* 2007 8:700–711
613 Available at: <https://www.nature.com/articles/nrn2201> [Accessed April 11, 2024].
- 614 Fox MD, Snyder AZ, Vincent JL, Corbetta M, Van Essen DC, Raichle ME (2005) The human
615 brain is intrinsically organized into dynamic, anticorrelated functional networks. *Proc*
616 *Natl Acad Sci U S A* 102:9673–9678 Available at:
617 <https://www.pnas.org/doi/abs/10.1073/pnas.0504136102> [Accessed April 11, 2024].
- 618 Golchert J, Smallwood J, Jefferies E, Seli P, Huntenburg JM, Liem F, Lauckner ME,
619 Oligschläger S, Bernhardt BC, Villringer A, Margulies DS (2017) Individual variation in
620 intentionality in the mind-wandering state is reflected in the integration of the default-
621 mode, fronto-parietal, and limbic networks. *Neuroimage* 146:226–235 Available at:
622 <https://www.sciencedirect.com/science/article/pii/S1053811916306425?via%3Dihub>
623 [Accessed July 31, 2018].
- 624 Gonzalez-Castillo J, Kam JWYY, Hoy CW, Bandettini PA (2021) How to Interpret Resting-
625 State fMRI: Ask Your Participants. *J Neurosci* 41:1130–1141 Available at:
626 <https://doi.org/10.1523/JNEUROSCI.1786-20.2020> [Accessed July 19, 2021].
- 627 Gratton C, Smith DM, Dorn M (2020) Digging Deeper to Chart the Landscape of Human
628 Brain Development. *Neuron* 106:209–211 Available at:
629 <https://doi.org/10.1016/j.neuron.2020.03.030> [Accessed February 15, 2022].
- 630 Greve DN, Fischl B (2009) Accurate and robust brain image alignment using boundary-

- 631 based registration. *Neuroimage* 48:63–72.
- 632 Hong SJ, de Wael RV, Bethlehem RAI, Lariviere S, Paquola C, Valk SL, Milham MP, Di
633 Martino A, Margulies DS, Smallwood J, Bernhardt BC (2019) Atypical functional
634 connectome hierarchy in autism. *Nat Commun* 10.
- 635 Hong SJ, Xu T, Nikolaidis A, Smallwood J, Margulies DS, Bernhardt B, Vogelstein J, Milham
636 MP (2020) Toward a connectivity gradient-based framework for reproducible biomarker
637 discovery. *Neuroimage* 223:117322.
- 638 Hsu WT, Rosenberg MD, Scheinost D, Constable RT, Chun MM (2018) Resting-state
639 functional connectivity predicts neuroticism and extraversion in novel individuals. *Soc*
640 *Cogn Affect Neurosci* 13:224–232 Available at:
641 <https://academic.oup.com/scan/article/13/2/224/4823668> [Accessed March 22, 2022].
- 642 Huang Z, Tarnal V, Vlisides PE, Janke EL, McKinney AM, Picton P, Mashour GA, Hudetz
643 AG (2021) Anterior insula regulates brain network transitions that gate conscious
644 access. *CellReports* 35:109081 Available at:
645 <https://doi.org/10.1016/j.celrep.2021.109081> [Accessed May 27, 2021].
- 646 Jenkinson M, Bannister P, Brady M, Smith S (2002) Improved Optimization for the Robust
647 and Accurate Linear Registration and Motion Correction of Brain Images. *Neuroimage*
648 17:825–841.
- 649 Jenkinson M, Beckmann CF, Behrens TEJ, Woolrich MW, Smith SM (2012) FSL.
650 *Neuroimage* 62:782–790 Available at:
651 <https://linkinghub.elsevier.com/retrieve/pii/S1053811911010603> [Accessed April 16,
652 2024].
- 653 Jenkinson M, Smith S (2001) A global optimisation method for robust affine registration of
654 brain images. *Med Image Anal* 5:143–156.
- 655 Johns MW (1991) A new method for measuring daytime sleepiness: the Epworth sleepiness
656 scale. *Sleep* 14:540–545 Available at: <https://europepmc.org/article/MED/1798888>
657 [Accessed September 24, 2021].
- 658 Joliffe IT (2002) *Principal Component Analysis*. New York: Springer-Verlag. Available at:
659 <http://link.springer.com/10.1007/b98835> [Accessed February 15, 2022].
- 660 Jones DN, Paulhus DL (2014) Introducing the Short Dark Triad (SD3): A Brief Measure of
661 Dark Personality Traits. *Assessment* 21:28–41 Available at: </record/2014-10974-004>
662 [Accessed September 24, 2021].
- 663 Jung CG (1995) *Memories, Dreams, Reflections*. In: *Memories, Dreams, Reflections*, pp
664 414–415. London: Fontana Press.
- 665 Kam JWY, Dao E, Farley J, Kevin F, Smallwood J, Schooler JW, Handy TC (2011) Slow
666 fluctuations in attentional control of sensory cortex. *J Cogn Neurosci* 23:460–470
667 Available at: <https://pubmed.ncbi.nlm.nih.gov/20146593/> [Accessed October 22, 2021].
- 668 Karapanagiotidis T, Jefferies E, Smallwood J (2021) Interactions between the neural
669 correlates of dispositional internally directed thought and visual imagery. *Philos Trans R*
670 *Soc B* 376:20190691 Available at:
671 <https://royalsocietypublishing.org/doi/abs/10.1098/rstb.2019.0691> [Accessed August 11,
672 2021].
- 673 Karapanagiotidis T, Vidaurre D, Quinn AJ, Vatansever D, Poerio GL, Turnbull A, Ho NSP,
674 Leech R, Bernhardt BC, Jefferies E, Margulies DS, Nichols TE, Woolrich MW,
675 Smallwood J (2020) The psychological correlates of distinct neural states occurring
676 during wakeful rest. *Sci Rep* 10 Available at: </pmc/articles/PMC7712889/> [Accessed

- 677 August 11, 2021].
- 678 Karapanagiotidis T, Vidaurre D, Quinn AJ, Vatansever D, Poerio GL, Turnbull A, Leech R,
679 Bernhardt B, Jefferies E, Margulies DS, Nichols TE, Woolrich MW, Smallwood J (2019)
680 Emergence of neural dynamics within a co-ordinate space of large-scale neural
681 hierarchies. *bioRxiv:2019.12.21.885772* Available at:
682 <https://www.biorxiv.org/content/10.1101/2019.12.21.885772v1> [Accessed January 20,
683 2020].
- 684 Koban L, Gianaros PJ, Kober H, Wager TD (2021) The self in context: brain systems linking
685 mental and physical health. *Nat Rev Neurosci* 2021 22:309–322 Available at:
686 <https://www.nature.com/articles/s41583-021-00446-8> [Accessed March 10, 2022].
- 687 Konu D, Mckeown B, Turnbull A, Siu Ping Ho N, Karapanagiotidis T, Vanderwal T, McCall C,
688 Tipper SP, Jefferies E, Smallwood J (2021) Exploring patterns of ongoing thought
689 under naturalistic and conventional task-based conditions. *Conscious Cogn* 93:103139.
- 690 Koo TK, Li MY (2016) A Guideline of Selecting and Reporting Intraclass Correlation
691 Coefficients for Reliability Research. *J Chiropr Med* 15:155 Available at:
692 </pmc/articles/PMC4913118/> [Accessed August 11, 2021].
- 693 Krieger-Redwood K, Jefferies E, Karapanagiotidis T, Seymour R, Nunes A, Ang JWA,
694 Majernikova V, Mollo G, Smallwood J (2016) Down but not out in posterior cingulate
695 cortex: Deactivation yet functional coupling with prefrontal cortex during demanding
696 semantic cognition. *Neuroimage* 141:366–377 Available at:
697 <https://pubmed.ncbi.nlm.nih.gov/27485753/> [Accessed September 24, 2021].
- 698 Kucyi A (2018) Just a thought: How mind-wandering is represented in dynamic brain
699 connectivity. *Neuroimage* 180:505–514.
- 700 Kucyi A, Esterman M, Capella J, Green A, Uchida M, Biederman J, Gabrieli JDE, Valera EM,
701 Whitfield-Gabrieli S (2021) Prediction of stimulus-independent and task-unrelated
702 thought from functional brain networks. *Nat Commun* 12:1–17 Available at:
703 <https://doi.org/10.1038/s41467-021-22027-0> [Accessed May 13, 2021].
- 704 Kuhl J, Kazén M (2009) *Persönlichkeits-Stil-und-Störungs-Inventar (PSSI): Manual* (Hogrefe,
705 ed).
- 706 Leech R, Braga R, Sharp DJ (2012) Echoes of the Brain within the Posterior Cingulate
707 Cortex. *J Neurosci* 32:215–222 Available at: <https://www.jneurosci.org/content/32/1/215>
708 [Accessed September 24, 2021].
- 709 Lynam DR, Smith GT, Whiteside SP, Cyders MA (2006) The UPPS-P: Assessing five
710 personality pathways to impulsive behavior. *West Lafayette, Purdue Univ* 10.
- 711 Marek S et al. (2022) Reproducible brain-wide association studies require thousands of
712 individuals. *Nature* 603:654 Available at: </pmc/articles/PMC8991999/> [Accessed
713 December 14, 2022].
- 714 Margulies DS, Ghosh SS, Goulas A, Falkiewicz M, Huntenburg JM, Langs G, Bezgin G,
715 Eickhoff SB, Castellanos FX, Petrides M, Jefferies E, Smallwood J (2016) Situating the
716 default-mode network along a principal gradient of macroscale cortical organization.
717 *Proc Natl Acad Sci U S A* 113:12574–12579 Available at:
718 <http://www.ncbi.nlm.nih.gov/pubmed/27791099> [Accessed December 11, 2019].
- 719 Mckeown B, Strawson WH, Wang HT, Karapanagiotidis T, Vos de Wael R, Benkarim O,
720 Turnbull A, Margulies D, Jefferies E, McCall C, Bernhardt B, Smallwood J (2020) The
721 relationship between individual variation in macroscale functional gradients and distinct
722 aspects of ongoing thought. *Neuroimage* 220:117072.

- 723 Mendes N et al. (2019) A functional connectome phenotyping dataset including cognitive
724 state and personality measures. *Sci Data* 6:180307 Available at:
725 <http://www.nature.com/articles/sdata2018307> [Accessed April 4, 2019].
- 726 Menon V (2011) Large-scale brain networks and psychopathology: a unifying triple network
727 model. *Trends Cogn Sci* 15:483–506 Available at: [https://pubmed-ncbi-nlm-nih-](https://pubmed-ncbi-nlm-nih-gov.browser.cbs.mpg.de/21908230/)
728 [gov.browser.cbs.mpg.de/21908230/](https://pubmed-ncbi-nlm-nih-gov.browser.cbs.mpg.de/21908230/) [Accessed March 10, 2022].
- 729 Müllensiefen D, Gingras B, Musil J, Stewart L (2014) Measuring the facets of musicality: The
730 Goldsmiths Musical Sophistication Index (Gold-MSI). *Pers Individ Dif* 60:S35.
- 731 O'Malley PM, Bachman JG (1979) Self-esteem and education: Sex and cohort comparisons
732 among high school seniors. *J Pers Soc Psychol* 37:1153–1159 Available at:
733 </record/1980-33361-001> [Accessed September 24, 2021].
- 734 Ophir E, Nass C, Wagner AD (2009) Cognitive control in media multitaskers. *Proc Natl Acad*
735 *Sci* 106:15583–15587 Available at: <https://www.pnas.org/content/106/37/15583>
736 [Accessed September 24, 2021].
- 737 Paquola C, Vos De Wael R, Wagstyl K, Bethlehem RAI, Hong S-J, Seidlitz J, Bullmore ET,
738 Evans AC, Misic B, Margulies DS, Smallwood J, Bernhardt BC (2019) Microstructural
739 and functional gradients are increasingly dissociated in transmodal cortices. Kennedy
740 H, ed. *PLoS Biol* 17:e3000284 Available at:
741 <http://dx.plos.org/10.1371/journal.pbio.3000284> [Accessed November 12, 2019].
- 742 Poerio GL, Sormaz M, Wang H-T, Margulies D, Jefferies E, Smallwood J (2017) The role of
743 the default mode network in component processes underlying the wandering mind. *Soc*
744 *Cogn Affect Neurosci* 12:1047–1062 Available at:
745 <http://www.ncbi.nlm.nih.gov/pubmed/28402561> [Accessed July 31, 2018].
- 746 R Core Team (2021) R: A language and environment for statistical computing. Available at:
747 <https://www.r-project.org/>.
- 748 Rokem A, Trumpis M, Pérez F (2009) In Proceedings of the 8th Python in Science
749 Conference (SciPy 2009). In: *SciPy Conference*, pp 68–75.
- 750 Schaefer A, Kong R, Gordon EM, Laumann TO, Zuo X-N, Holmes AJ, Eickhoff SB, Yeo BTT
751 (2018) Local-Global Parcellation of the Human Cerebral Cortex from Intrinsic Functional
752 Connectivity MRI. *Cereb Cortex* 28:3095–3114 Available at: [https://academic-oup-](https://academic-oup-com.browser.cbs.mpg.de/cercor/article/28/9/3095/3978804)
753 [com.browser.cbs.mpg.de/cercor/article/28/9/3095/3978804](https://academic-oup-com.browser.cbs.mpg.de/cercor/article/28/9/3095/3978804) [Accessed August 11,
754 2021].
- 755 Schmidt RE, Gay P, D'Acremont M, Van Der Linden M (2008) A German adaptation of the
756 upps impulsive behavior scale: Psychometric properties and factor structure. *Swiss J*
757 *Psychol* 67:107–112 Available at:
758 [http://psycontent.metapress.com/openurl.asp?genre=article&id=doi:10.1024/1421-](http://psycontent.metapress.com/openurl.asp?genre=article&id=doi:10.1024/1421-0185.67.2.107)
759 [0185.67.2.107](http://psycontent.metapress.com/openurl.asp?genre=article&id=doi:10.1024/1421-0185.67.2.107) [Accessed June 5, 2014].
- 760 Smallwood J (2013a) Distinguishing how from why the mind wanders: A process-occurrence
761 framework for self-generated mental activity. *Psychol Bull* 139:519–535.
- 762 Smallwood J (2013b) Searching for the elements of thought: Reply to franklin, mrazek,
763 broadway, and schooler (2013). *Psychol Bull* 139:542–547.
- 764 Smallwood J, Beach E, Schooler JW, Handy TC (2008) Going AWOL in the Brain: Mind
765 Wandering Reduces Cortical Analysis of External Events. *J Cogn Neurosci* 20:458–
766 469.
- 767 Smallwood J, Bernhardt BC, Leech R, Bzdok D, Jefferies E, Margulies DS (2021a) The
768 default mode network in cognition: a topographical perspective. *Nat Rev Neurosci*

- 769 2021:1–11 Available at: <https://www-nature-com.browser.cbs.mpg.de/articles/s41583-770>
770 021-00474-4 [Accessed July 7, 2021].
- 771 Smallwood J, Karapanagiotidis T, Ruby F, Medea B, de Caso I, Konishi M, Wang H-T,
772 Hallam G, Margulies DS, Jefferies E (2016) Representing Representation: Integration
773 between the Temporal Lobe and the Posterior Cingulate Influences the Content and
774 Form of Spontaneous Thought Biagini G, ed. PLoS One 11:e0152272 Available at:
775 <http://dx.plos.org/10.1371/journal.pone.0152272> [Accessed May 28, 2018].
- 776 Smallwood J, Turnbull A, Wang H ting, Ho NSP, Poerio GL, Karapanagiotidis T, Konu D,
777 Mckeown B, Zhang M, Murphy C, Vatansever D, Bzdok D, Konishi M, Leech R, Seli P,
778 Schooler JW, Bernhardt B, Margulies DS, Jefferies E (2021b) The neural correlates of
779 ongoing conscious thought. *iScience* 24:102132.
- 780 Sormaz M, Murphy C, Wang H, Hymers M, Karapanagiotidis T, Poerio G, Margulies DS,
781 Jefferies E, Smallwood J (2018) Default mode network can support the level of detail in
782 experience during active task states. *Proc Natl Acad Sci U S A* 115:9318–9323
783 Available at: <http://www.ncbi.nlm.nih.gov/pubmed/30150393> [Accessed April 17, 2019].
- 784 Spisak T, Bingel U, Wager TD (2023) Multivariate BWA can be replicable with moderate
785 sample sizes. *Nature* 615:E4–E7 Available at: <https://www.nature.com/articles/s41586-786>
786 023-05745-x [Accessed March 31, 2023].
- 787 Storey JD (2003) The positive false discovery rate: a Bayesian interpretation and the q-
788 value. <https://doi.org/10.1214/aos/1074290335> 31:2013–2035 Available at:
789 [https://projecteuclid.org/journals/annals-of-statistics/volume-31/issue-6/The-positive-
790 false-discovery-rate--a-Bayesian-interpretation-and/10.1214/aos/1074290335.full](https://projecteuclid.org/journals/annals-of-statistics/volume-31/issue-6/The-positive-false-discovery-rate--a-Bayesian-interpretation-and/10.1214/aos/1074290335.full)
791 [Accessed November 8, 2021].
- 792 Tangney JP, Baumeister RF, Boone AL (2004) High self-control predicts good adjustment,
793 less pathology, better grades, and interpersonal success. *J Pers* 72:271–324 Available
794 at: <https://pubmed.ncbi.nlm.nih.gov/15016066/> [Accessed September 24, 2021].
- 795 Tuckman BW (2016) The Development and Concurrent Validity of the Procrastination Scale:
796 <http://dx.doi.org/10.1177/0013164491512022> 51:473–480 Available at:
797 <https://journals.sagepub.com/doi/10.1177/0013164491512022> [Accessed September
798 24, 2021].
- 799 Turnbull A, Garfinkel SN, Ho NSP, Critchley HD, Bernhardt BC, Jefferies E, Smallwood J
800 (2020a) Word up – Experiential and neurocognitive evidence for associations between
801 autistic symptomology and a preference for thinking in the form of words. *Cortex*
802 128:88–106.
- 803 Turnbull A, Karapanagiotidis T, Wang HT, Bernhardt BC, Leech R, Margulies D, Schooler J,
804 Jefferies E, Smallwood J (2020b) Reductions in task positive neural systems occur with
805 the passage of time and are associated with changes in ongoing thought. *Sci Rep* 10
806 Available at: [/pmc/articles/PMC7303126/?report=abstract](https://pubmed.ncbi.nlm.nih.gov/34312672/) [Accessed November 11,
807 2020].
- 808 Turnbull A, Wang H-T, Schooler JW, Jefferies E, Margulies DS, Smallwood J (2019a) The
809 ebb and flow of attention: Between-subject variation in intrinsic connectivity and
810 cognition associated with the dynamics of ongoing experience. *Neuroimage* 185:286–
811 299 Available at:
812 <https://www.sciencedirect.com/science/article/pii/S1053811918319414?via%3Dihub>
813 [Accessed January 18, 2019].
- 814 Turnbull A, Wang H, Murphy C, Ho NSP, Wang X, Sormaz M, Karapanagiotidis T, Leech
815 RM, Bernhardt B, Margulies DS, Vatansever D, Jefferies E, Smallwood J (2019b) Left
816 dorsolateral prefrontal cortex supports context-dependent prioritisation of off-task

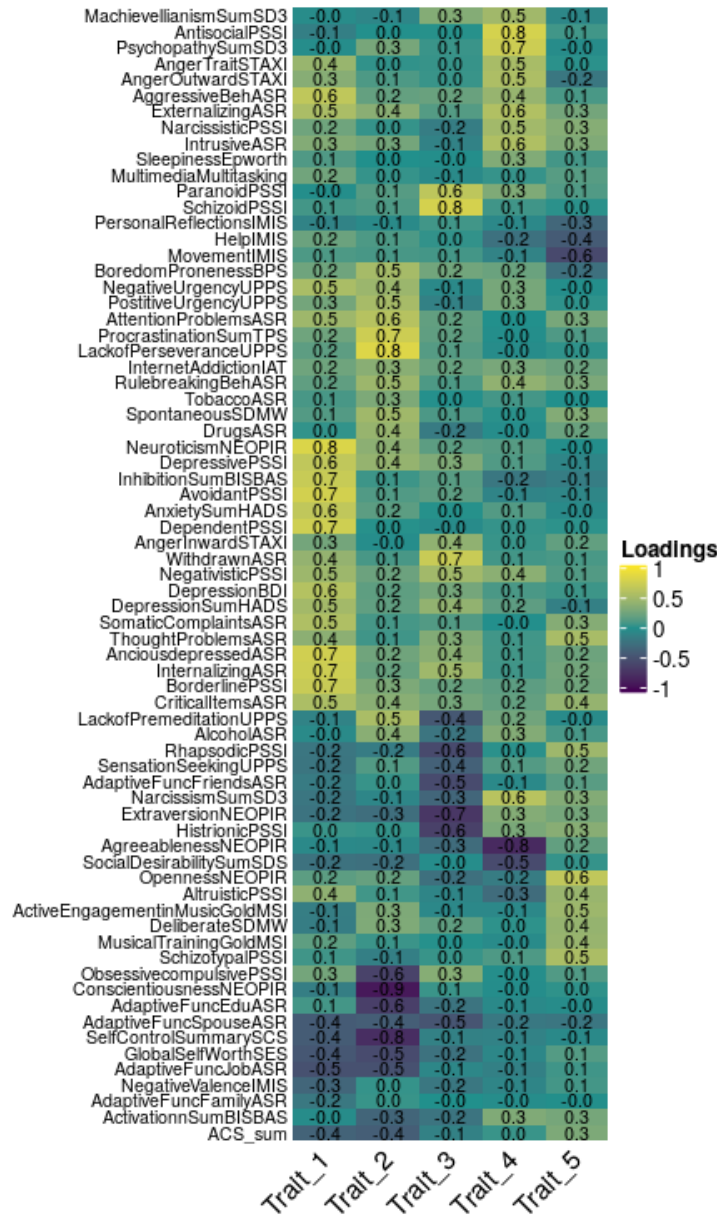
- 817 thought. *Nat Commun* 10:3816 Available at: [http://www.nature.com/articles/s41467-](http://www.nature.com/articles/s41467-019-11764-y)
818 019-11764-y [Accessed November 12, 2019].
- 819 Van Essen DC, Smith SM, Barch DM, Behrens TEJ, Yacoub E, Ugurbil K, Consortium for
820 the W-MH (2013) The WU-Minn Human Connectome Project: An Overview.
821 *Neuroimage* 80:62 Available at: [/pmc/articles/PMC3724347/](https://pubmed.ncbi.nlm.nih.gov/29078345/) [Accessed August 12,
822 2021].
- 823 Vanhaudenhuyse A, Demertzi A, Schabus M, Noirhomme Q, Bredart S, Boly M, Phillips C,
824 Soddu A, Luxen A, Moonen G, Laureys S (2011) Two distinct neuronal networks
825 mediate the awareness of environment and of self. *J Cogn Neurosci* 23:570–578
826 Available at: <https://pubmed.ncbi.nlm.nih.gov/20515407/> [Accessed April 11, 2024].
- 827 Vatansever D, Menon DK, Stamatakis EA (2017) Default mode contributions to automated
828 information processing. *Proc Natl Acad Sci U S A* 114:12821–12826 Available at:
829 <http://www.ncbi.nlm.nih.gov/pubmed/29078345> [Accessed April 29, 2019].
- 830 Vos de Wael R, Benkarim O, Paquola C, Lariviere S, Royer J, Tavakol S, Xu T, Hong S-J,
831 Langs G, Valk S, Mistic B, Milham M, Margulies D, Smallwood J, Bernhardt BC (2020)
832 BrainSpace: a toolbox for the analysis of macroscale gradients in neuroimaging and
833 connectomics datasets. *Commun Biol* 2020 31 3:1–10 Available at:
834 <https://www.nature.com/articles/s42003-020-0794-7> [Accessed November 3, 2021].
- 835 Wang H-T, Ho NSP, Bzdok D, Bernhardt BC, Margulies DS, Jefferies E, Smallwood J (2020)
836 Neurocognitive patterns dissociating semantic processing from executive control are
837 linked to more detailed off-task mental time travel. *Sci Reports* 2020 101 10:1–14
838 Available at: <https://www.nature.com/articles/s41598-020-67605-2> [Accessed
839 September 24, 2021].
- 840 Wang H-TT, Poerio G, Murphy C, Bzdok D, Jefferies E, Smallwood J (2018) Dimensions of
841 Experience: Exploring the Heterogeneity of the Wandering Mind. *Psychol Sci* 29:56–71
842 Available at: <http://www.ncbi.nlm.nih.gov/pubmed/29131720> [Accessed July 31, 2018].
- 843 Wen X, He H, Dong L, Chen J, Yang J, Guo H, Luo C, Yao D (2020) Alterations of local
844 functional connectivity in lifespan: A resting-state fMRI study. *Brain Behav* 10:e01652
845 Available at: <https://onlinelibrary.wiley.com/doi/full/10.1002/brb3.1652> [Accessed March
846 21, 2022].
- 847 Worsley KJ, Taylor JE, Carbonell F, Chung MK, Duerden E, Bernhardt B, Lyttelton O,
848 Boucher M, Evans AC (2009) SurfStat: A Matlab toolbox for the statistical analysis of
849 univariate and multivariate surface and volumetric data using linear mixed effects
850 models and random field theory. *Neuroimage* 47 Available at:
851 <http://www.stat.uchicago.edu/~worsley/surfstat/poster.htm> [Accessed August 11, 2021].
- 852 Yarkoni T, Poldrack RA, Nichols TE, Van Essen DC, Wager TD, T Y, RA P, TE N, DC VE,
853 TD W (2011) Large-scale automated synthesis of human functional neuroimaging data.
854 8:665–670 Available at: [https://pubmed-ncbi-nlm-nih-](https://pubmed.ncbi.nlm.nih.gov/21706013/)
855 [gov.brower.cbs.mpg.de/21706013/](https://pubmed.ncbi.nlm.nih.gov/21706013/) [Accessed August 11, 2021].
- 856 Yeo BTT, Krienen FM, Sepulcre J, Sabuncu MR, Lashkari D, Hollinshead M, Roffman JL,
857 Smoller JW, Zöllei L, Polimeni JR, Fisch B, Liu H, Buckner RL (2011) The organization
858 of the human cerebral cortex estimated by intrinsic functional connectivity. *J*
859 *Neurophysiol* 106:1125–1165 Available at:
860 <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3174820/> [Accessed March 30, 2021].
- 861 Young KS (1998) Internet Addiction: The Emergence of a New Clinical Disorder.
862 *CyberPsychology Behav* 1:237–244 Available at:
863 <https://www.liebertpub.com/doi/abs/10.1089/cpb.1998.1.237> [Accessed September 24,
864 2021].

865 Zhang J, Kucyi A, Raya J, Nielsen AN, Nomi JS, Damoiseaux JS, Greene DJ, Horovitz SG,
866 Uddin LQ, Whitfield-Gabrieli S (2021) What have we really learned from functional
867 connectivity in clinical populations? *Neuroimage* 242:118466 Available at:
868 <https://linkinghub.elsevier.com/retrieve/pii/S1053811921007394> [Accessed August 25,
869 2021].

870 Zigmond AS, Snaith RP (1983) The hospital anxiety and depression scale. *Acta Psychiatr*
871 *Scand* 67:361–370 Available at: <https://pubmed.ncbi.nlm.nih.gov/6880820/> [Accessed
872 September 24, 2021].

873

874 Supplementary Figures



875

876 **Supplementary Figure 1. Heatmap showing variable component loadings for the first 5**

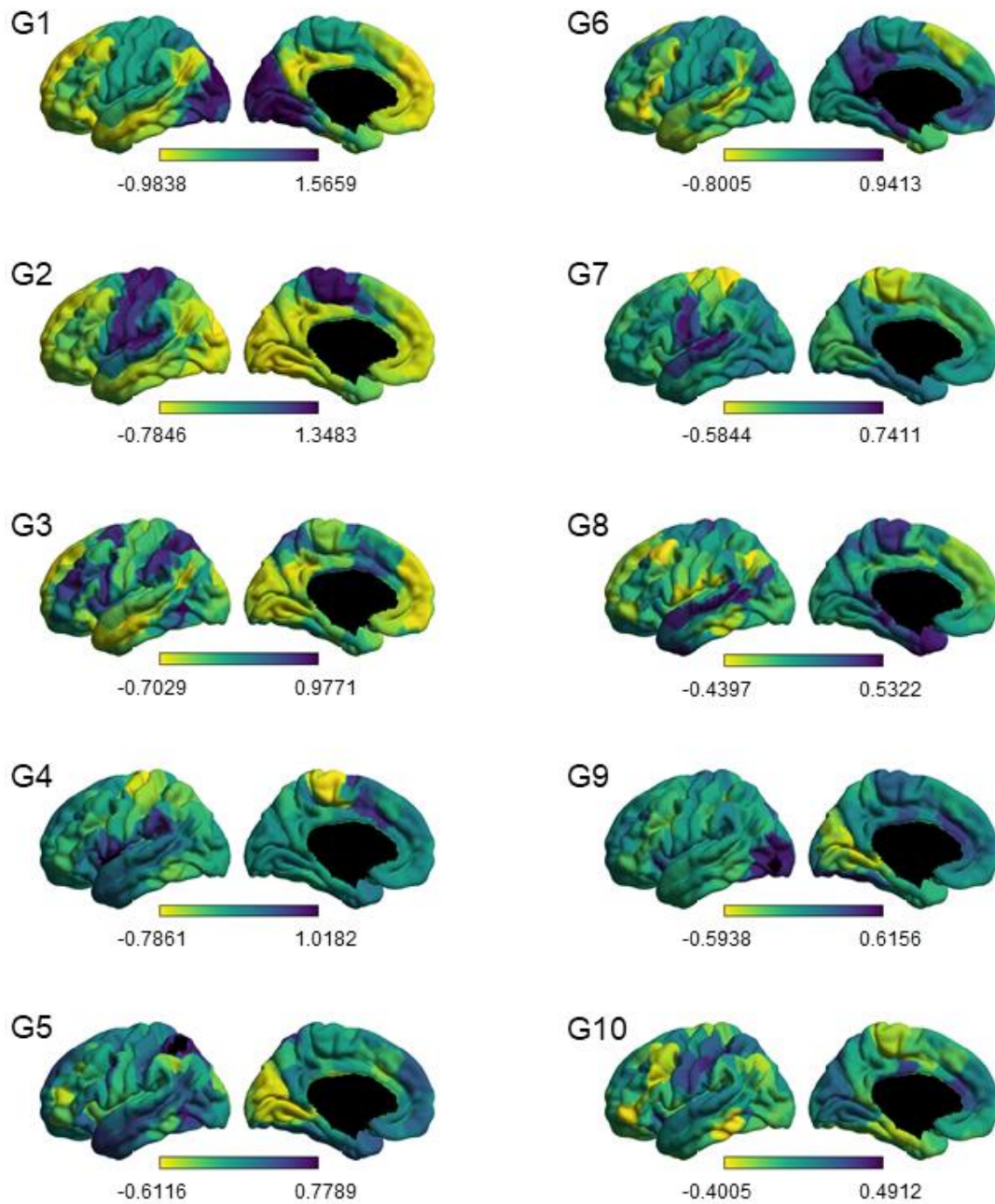
877 **principal components derived from trait questionnaires**



878

879 **Supplementary Figure 2. Heatmap showing variable component loadings for the first 5**

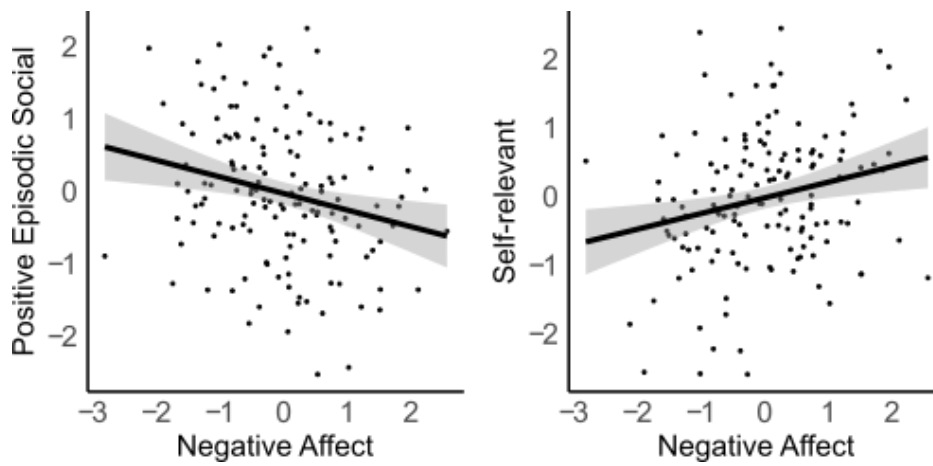
880 **principal components derived from MDES**



881

882 **Supplementary figure 3. Ten group-level cortical gradients shown from the left lateral**
883 **and medial views.**

884



885

886 **Supplementary Figure 4. Scatter-plots showing the relationship between trait “Negative**
887 **affect”, and “Positive Episodic Social” and “Self-relevant” thought.**

888