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1 The relationship between individual variation in macroscale functional gradients and distinct

2 aspects of ongoing thought.

3

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18   **Abstract**

19   Contemporary accounts of ongoing thought recognise it as a heterogeneous and
20   multidimensional construct, varying in both form and content. An emerging body of evidence
21   demonstrates that distinct types of experience are associated with unique neurocognitive
22   profiles, that can be described at the whole-brain level as interactions between multiple large-
23   scale networks. The current study sought to explore the possibility that whole-brain functional
24   connectivity patterns at rest may be meaningfully related to patterns of ongoing thought that
25   occurred over this period. Participants underwent resting-state functional magnetic resonance
26   imaging (rs-fMRI) followed by a questionnaire retrospectively assessing the content and form
27   of their ongoing thoughts during the scan. A non-linear dimension reduction algorithm was
28   applied to the rs-fMRI data to identify components explaining the greatest variance in whole-
29   brain connectivity patterns, and ongoing thought patterns during the resting-state were
30   measured retrospectively at the end of the scan. Multivariate analyses revealed that
31   individuals for whom the connectivity of the sensorimotor system was maximally distinct from
32   the visual system were most likely to report thoughts related to finding solutions to problems
33   or goals and least likely to report thoughts related to the past. These results add to an
34   emerging literature that suggests that unique patterns of experience are associated with
35   distinct distributed neurocognitive profiles and highlight that unimodal systems may play an
36   important role in this process.

37

1 Introduction

When unoccupied by events in the immediate environment, such as during the so-called resting-state, humans often spend substantial amounts of time focused on information that is relevant to themselves but absent from the here and now. These self-generated experiences can be a source of unhappiness and distress (Killingsworth & Gilbert, 2010; Poerio et al., 2013). However, they can also allow individuals to mentally reframe their goals in a more concrete way (Medea et al., 2018), and reduce loneliness (Poerio et al., 2015), perhaps because of links between self-generated thought with creativity (Baird et al., 2012; Gable et al., 2019; Smeekens & Kane, 2016; Wang et al., 2018), social problem solving (Ruby et al., 2013), or generation of information based on semantic knowledge (Wang et al., 2019). Understanding the neural basis of these different patterns of ongoing thoughts, is therefore an important goal for cognitive neuroscience because it may help describe the underlying neural architecture which supports aspects of human cognition that are both beneficial and detrimental to health and well-being. In this study we examined whether an individual's ongoing thought patterns could predict individual variation in their functional organization at rest.

Contemporary views on how the structure of the cortex constrains its functions have identified the important roles that macroscale patterns of cortical organization play in determining cognition (Mesulam, 1998, Margulies et al., 2016). These patterns, or motifs, can be well captured by dimension reduction techniques that identify low-dimensional manifold spaces, often referred to as 'cortical gradients'. This approach has been important in characterising the axis upon which cortical structure is organised (Paquola et al., 2019; Vazquez-Rodriguez et al., 2019), how the specific topological features of the cortex give rise to different functional hierarchies (Margulies et al., 2016), describing changes in brain function in developmental disorders (Hong et al., 2019) and across primate species (Xu et al., 2019) and capturing dynamic changes between states of external task focus and self-generated social episodic thought (Turnbull et al., in press). One advantage of gradient approaches to neural function is that they describe multivariate whole-brain patterns of organization (i.e. the relationship between different neural systems) and so allow the investigation of whether macroscale features of cortical organization relate to features of cognition. This approach is particularly useful for understanding features of higher-order cognition which are hypothesised to depend upon the interaction between multiple neural systems (e.g. Smallwood et al., 2011; Smallwood & Schooler, 2015; Jefferies et al., 2020).

75   Our current study, therefore, explores the possibility that macroscale properties of the cortex
76   captured by low-dimensional descriptors of functional organization at rest are related to
77   individual variation in ongoing experience that emerge during this period. Resting-state fMRI
78   was used to record patterns of intrinsic neural activity in a large cohort (N=277). We employed
79   the BrainSpace toolbox (Vos de Wael et al., 2019) to calculate the dimensions that
80   characterise the functional connectivity of the brain at rest. At the end of the scan, participants
81   completed a questionnaire that retrospectively assessed their experiences during the scan.
82   The questions were based on those used in previous studies exploring population variation in
83   functional connectivity and aimed at capturing the heterogeneity of ongoing thought
84   (Karapanagiotidis et al., 2017; Smallwood et al., 2016). While retrospective experience-
85   sampling sacrifices temporal specificity, it is particularly beneficial for understanding the neural
86   basis of ongoing experience because the absence of interruptions ensures that neural
87   dynamics unfold in a relatively natural way (Smallwood & Schooler, 2015). Using these data,
88   we examined whether specific types of thought measured at the end of the scan were
89   predictive of individual variation along low-dimensional gradients of macroscale functional
90   connectivity at rest. These data have previously been examined by Karapanagiotidis et al.
91   (2019) who applied Hidden Markov modelling to identify neural states occurring at rest. They
92   found states linked to autobiographical planning and intrusive rumination that were related to
93   differences in the relative dominance of frontoparietal and motor systems, and default mode
94   and visual systems.
95
96   Prior studies have highlighted three cortical gradients which each relate to meaningful features
97   of cognition. The first gradient describes the difference between regions of unimodal and
98   transmodal cortex (Margulies et al., 2016). Studies have shown that this neural motif is
99   observed when participants must use information from memory to guide behaviour, such as
100 when visuospatial decisions must be made with previously encountered information rather
101 than immediate perceptual information (Murphy et al., 2018, 2019). The second gradient is
102 related to the dissociation between unimodal systems concerned with vision and sensorimotor
103 systems (Margulies et al., 2016). Finally, the third gradient describes a distinction between the
104 so-called default mode and task-positive systems. This pattern is often observed when
105 researchers compare easy and demanding cognitive tasks (Cole et al., 2013; Duncan, 2010).
106 Prior studies have shown that this pattern is linked to the difference between on and off task
107 states and that this distinction also helps describe neurocognitive changes related to the
108 passage of time (Turnbull et al., in press). Our study aimed to explore whether any of these
109 macroscale neural motifs were related to the participants reports at the end of the experimental
110 session.

4

2 Methods

2.1 Participants

Two hundred and seventy-seven healthy participants were recruited from the University of York. Written informed consent was obtained for all participants and the study was approved by the York Neuroimaging Centre Ethics Committee. Twenty-three participants were excluded from analyses; two due to technical issues during the neuroimaging data acquisition and twenty-one for excessive movement during the fMRI scan (mean framewise displacement (Power et al., 2014) > 0.3 mm and/or more than 15% of their data affected by motion), resulting in a final cohort of n = 254 (169 females, mean ± SD age = 20.7±2.4 years). The questionnaire and functional MRI data in this study are the same as those reported in Karapanagiotidis et al. (2019).

2.2 Data and Code availability

Gradient maps one to ten from the group-averaged dimension reduction analysis described in section 2.5.3 below are publicly available on NeuroVault in a collection with the title of this article (https://neurovault.org/collections/6746/). Raw fMRI and questionnaire data are restricted in accordance with ERC and EU regulations. All code used in the production of this manuscript is publicly available online in the following repository: https://github.com/Bronte-Mckeown/GradientAnalysis.

2.3 Retrospective experience-sampling

Participants' experience during the resting-state fMRI scan was sampled by asking them to retrospectively report their thoughts during the resting-state period at the end of the scan. Experience was measured using a 4-point Likert scale with the question order randomised (all 25 questions are shown in Table 1).

Table 1. 25-item experience-sampling questionnaire completed at the end of the resting-state fMRI scan. Answers were given on a 4-point Likert scale ranging from "Not at all" to "Completely".

Dimension	Question (My thoughts…)
Vivid	… were vivid as if I was there
Normal	… were similar to thoughts I often have
Future	… involved future events
Negative	… were about something negative
Detail	… were detailed and specific
Words	… were in the form of words
Evolving	… tended to evolve in a series of steps
Spontaneous	… were spontaneous
Positive	… were about something positive
Images	… were in the form of images
People	… involved other people
Past	… involved past events
Deliberate	… were deliberate
Self	… involved myself
Stop	… were hard for me to stop
Distant time	… were related to a more distant time
Abstract	… were about ideas rather than events or objects
Decoupled	… dragged my attention away from the external world
Important	… were on topics that I care about
Intrusive	… were intrusive
Problem Solving	… were about solutions to problems (or goals)
Here and Now	… were related to the here and now
Creative	… gave me a new insight into something I have thought about before
Realistic	… were about an event that has happened or could take place
Same Theme	… at different points in time were all on the same theme

134

2.4 Procedure

136 All participants underwent a 9-minute resting-state fMRI scan. During the scan, they were
137 instructed to passively view a fixation cross and not to think of anything in particular.

138 Immediately following the scan, they completed the 25-item experience-sampling
139 questionnaire while still in the scanner.

140 2.5 Resting-state fMRI

141 2.5.1 MRI data acquisition

142 MRI data were acquired on a GE 3 Tesla Signa Excite HDxMRI scanner, equipped with an
143 eight-channel phased array head coil at York Neuroimaging Centre, University of York. For
144 each participant, we acquired a sagittal isotropic 3D fast spoiled gradient-recalled echo T1-
145 weighted structural scan (TR = 7.8 ms, TE = minimum full, flip angle = 20°, matrix = 256x256,
146 voxel size = 1.13x1.13x1 mm3, FOV = 289x289 mm2). Resting-state fMRI data based on
147 blood oxygen level-dependent contrast images with fat saturation were acquired using a
148 gradient single-shot echo-planar imaging sequence (TE = minimum full (≈19 ms), flip angle =
149 90°, matrix = 64x64, FOV = 192x192 mm2, voxel size = 3x3x3 mm3, TR = 3000 ms, 60 axial
150 slices with no gap and slice thickness of 3 mm). Scan duration was 9 minutes which allowed
151 us to collect 180 whole-brain volumes. These acquisition details are identical to the ones
152 described in Karapanagiotidis et al. (2019).

153 2.5.2 MRI data pre-processing

154 fMRI data pre-processing was performed using SPM12
155 (http://www.fil.ion.ucl.ac.uk/spm) and the CONN toolbox (v.18b)
156 (https://www.nitrc.org/projects/conn) (Whitfield-Gabrieli & Nieto-Castanon, 2012)
157 implemented in Matlab (R2018a) (https://uk.mathworks.com/products/matlab). Pre-
158 processing steps followed CONN's default pipeline and included motion estimation and
159 correction by volume realignment using a six-parameter rigid body transformation, slice-time
160 correction, and simultaneous grey matter (GM), white matter (WM) and cerebrospinal fluid
161 (CSF) segmentation and normalisation to MNI152 stereotactic space (2 mm isotropic) of both
162 functional and structural data. Following pre-processing, the following potential confounders
163 were statistically controlled for: 6 motion parameters calculated at the previous step and their
164 1st and 2nd order derivatives, volumes with excessive movement (motion greater than 0.5
165 mm and global signal changes larger than $z = 3$), linear drifts, and five principal components
166 of the signal from WM and CSF (CompCor approach) (Behzadi et al., 2007). Finally, data were
167 band-pass filtered between 0.01 and 0.1 Hz. No global signal regression was performed. The
168 pre-processing steps reported here are identical to the ones described in Karapanagiotidis et
169 al. (2019).

2.5.3 Whole-brain Functional Connectivity: Dimension reduction

Following pre-processing, the functional time-series from 400 ROIs based on the 400 Schaefer parcellation (Schaefer et al., 2018) were extracted for each individual. A connectivity matrix for each individual was then calculated using Pearson correlation resulting in a 400x400 connectivity matrix for each participant. These individual connectivity matrices were then averaged to calculate a group-averaged connectivity matrix. The Brainspace Toolbox (Vos de Wael et al., 2019) was then used to extract ten group-level gradients from the group-averaged connectivity matrix (dimension reduction technique = diffusion embedding, kernel = normalized angle, sparsity = 0.9). Although we were only interested in the first three gradients as they all have reasonably well described functional associations, we extracted ten gradients to maximise the degree of fit between the group-averaged gradients and the individual-level gradients (see Inline Supplementary Table 1 for the average degree of fit for gradients one to three when extracting ten gradients compared to three). These group-averaged gradients act as a template to which individual gradients can be compared, to allow an investigation of individual differences along each gradient in the current sample. The variance explained by each group-averaged gradient one to ten is shown in Inline Supplementary Figure 1.

The group-level gradient solutions were aligned using Procrustes rotation to a subsample of the HCP dataset ([n=217, 122 women, mean $\pm$ sd age = 28.5 $\pm$ 3.7 y]; for full details of subject selection see Vos de Wael et al. (2018)) openly available within the Brainspace toolbox (Vos de Wael et al., 2019). This alignment step improves the stability of the group-level gradient templates by maximising the comparability of the solutions to those from the existing literature (i.e. Margulies et al., 2016). The first three group-averaged gradients, with and without alignment to the HCP data are shown in Inline Supplementary Figure 2. To demonstrate the benefits of this alignment step, we calculated the similarity using Spearman Rank correlation between the first five aligned and unaligned group-level gradients with the first five gradients reported in Margulies et al. (2016) which were calculated using 820 participants over an hour resting-state scan. Aligning our gradients with a subsample of the HCP data increased the similarity between our gradients and Margulies' et al (2016) gradients (see Inline Supplementary Table 2).

Using identical parameters, individual-level gradients were then calculated for each individual using their 400x400 connectivity matrix. These individual-level gradient maps were aligned to the group-level gradient maps using Procrustes rotation to improve comparison between the group-level gradients and individual-level gradients (N iterations = 10). This analysis resulted in ten group-level gradients and ten individual-level gradients for each participant explaining

maximal whole-brain connectivity variance in descending order. All ten group-level gradients are shown in Figure 1, however, only the first three gradients were retained for further analysis. To demonstrate the variability of individual-level gradients, Inline Supplementary Figure 3 shows the highest, lowest and median similarity gradient maps for gradients one to three.
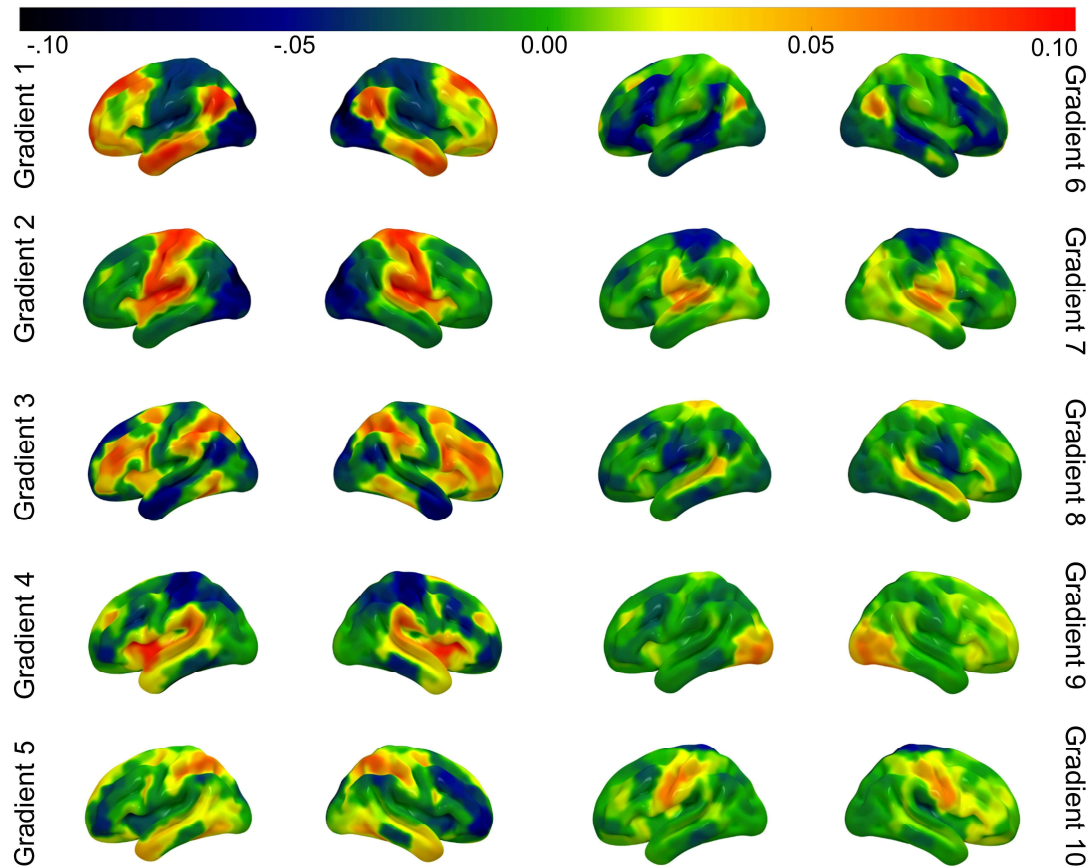

Figure 1. *Group-averaged gradients one to ten (left and right lateral views) explaining maximal variance in whole-brain connectivity patterns.* Regions that share similar connectivity profiles fall together along each gradient (similar colours) and regions that have more distinct connectivity profiles fall further apart (different colours). The positive and negative loading is arbitrary. Regions which fall at the extreme end of each gradient have the greatest dissimilarity in their connectivity profiles. Only gradients one to three were included in the multivariate analysis. These ten group-averaged gradient maps are publicly available on NeuroVault (https:/neurovault.org/collections/6746/).

2.5.4 Individual-level Similarity Analysis: Spearman's Rank Correlation

In order to investigate individual differences for each of the three connectivity gradients, a Spearman's rank correlation was used to calculate the extent to which each individual-level

223 gradient was related to each group-level gradient. In this way, the correlation coefficient
224 calculated for each participant for gradients one to three is used as a second-order statistic
225 indicating the similarity between the group-level and individual-level gradients. Fishers R-to-Z
226 transformation was applied to these correlation coefficient scores. These z-transformed
227 regression coefficients will be referred to as 'gradient similarity scores' from this point onwards.
228 These similarity scores were then entered as dependent variables in subsequent multivariate
229 regression analyses to investigate whether individual variation in ongoing thought patterns
230 could predict individual variation along the first three whole-brain connectivity gradients. A
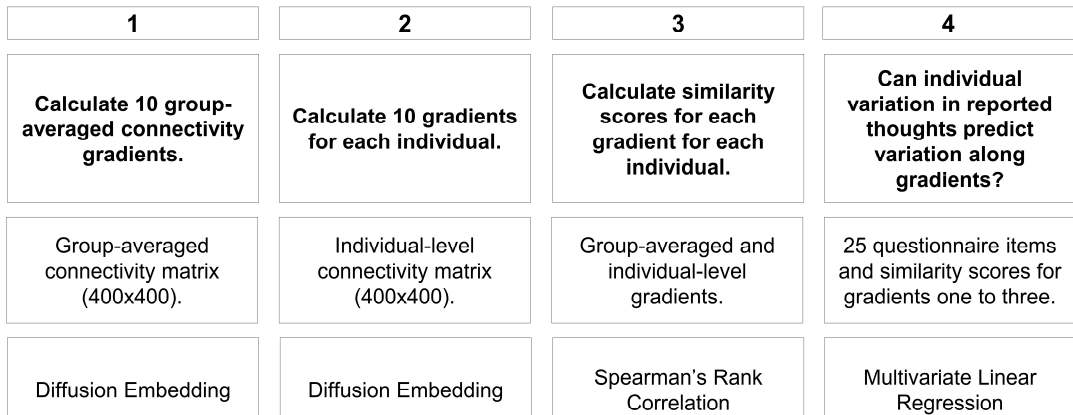231 schematic for the analysis pipeline is shown in Figure 2.

1	2	3	4
Calculate 10 group-averaged connectivity gradients.	Calculate 10 gradients for each individual.	Calculate similarity scores for each gradient for each individual.	Can individual variation in reported thoughts predict variation along gradients?
Group-averaged connectivity matrix (400x400).	Individual-level connectivity matrix (400x400).	Group-averaged and individual-level gradients.	25 questionnaire items and similarity scores for gradients one to three.
Diffusion Embedding	Diffusion Embedding	Spearman's Rank Correlation	Multivariate Linear Regression

232
233
234 **Figure 2.** *Summary of the analysis pipeline*. Numbers represent order of step. Top panel in
235 bold describes the overarching goal of each step. Middle panel specifies the data being used.
236 Bottom panel indicates which analysis or statistical test was used to achieve the step.

237 # 3 Results

238 ## 3.1 Experience-sampling responses

239 The experience-sampling data is summarised in figure 3, revealing the distribution of
240 responses for each item as well as the covariance between each item. While some
241 questionnaire items are significantly correlated, the variance inflation factor for each
242 questionnaire item was <2, indicating that multicollinearity is not a concern in the multivariate
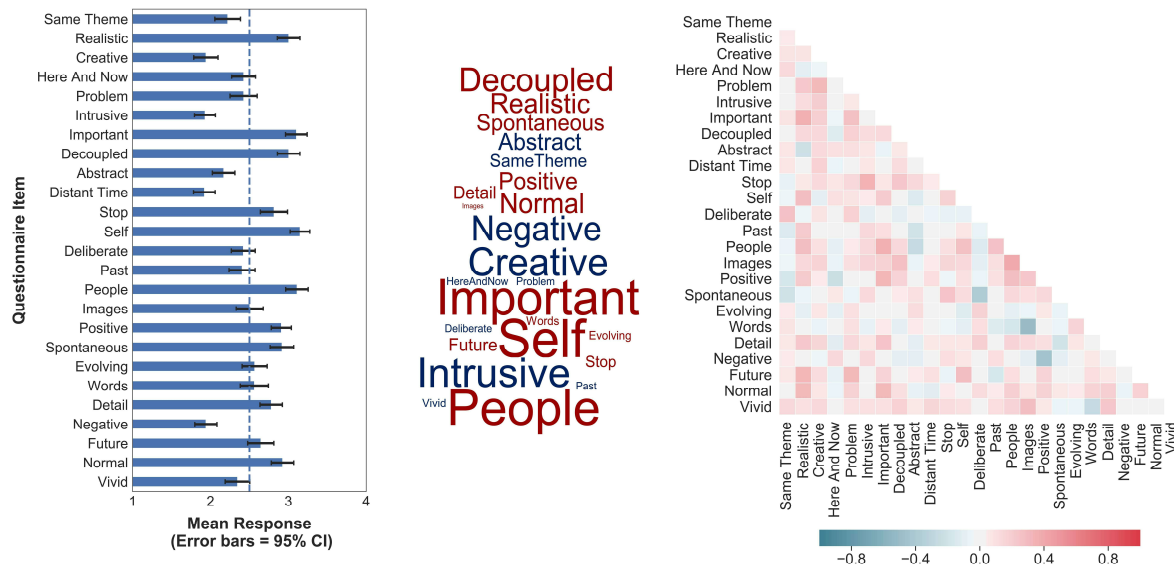243 regression analysis described below.

244 **Figure 3**. *Summary information describing the distribution of the retrospective measures of*
245 *ongoing experience recorded in our study*. In the left-hand panel, the bar graph shows the
246 average loading on each question relative to the mid-point of the scale (indicated by the
247 dashed line). The error bars reflect 95% confidence intervals, adjusted to account for family-
248 wise error (i.e. the 25 items). The word cloud shows this information in a different form in
249 which the size of the word describes its distance from the mid-point and its colour (cold /
250 warm) reflects its loading. The right-hand panel illustrates the patterns of covariation
251 between these items (Pairwise Pearson correlation).

252 ## 3.2 Multivariate analysis

253 We examined whether there was any relationship between the low-dimensional
254 representations of the macroscale organization of neural function and the experience of
255 participants during the scanning. We used a Multivariate linear regression (SPSS; version 26)
256 in which individual items from the experience-sampling questionnaire were included as
257 explanatory variables and the similarity scores for gradients one to three were entered as
258 dependent variables. Age, gender and mean movement during the scan were entered as
259 nuisance covariates. This analysis revealed that there was a multivariate effect for the
260 'problem-solving' item [Pillai's trace = .046, $F_{(3, 223)}$ = 3.54, p = .015] and the 'past' item
261 [Pillai's trace = .051, $F_{(3, 223)}$ = 3.97, p = .009]. These results establish that these two aspects
262 of the questionnaire varied significantly with the similarity scores for the functional motifs
263 apparent at rest.

264

265   We calculated the parameter estimates for these multivariate effects linked to thoughts of the
266   'past' (Gradient one (b = -0.018, 95% CI = [-0.042, 0.006], p = .137), Gradient two (b = -0.032,
267   95% CI = [-0.056, -0.008], p = .009) and Gradient three (b = 0.006, 95% CI = [-0.011, 0.024],
268   p = .490) and for 'problem-solving' (Gradient one (b = 0.020, 95% CI = [-0.005, 0.044], p =
269   .112), Gradient two (b = 0.036, 95% CI = [0.011, 0.061], p = .004) and Gradient three (b = -
270   001, 95% CI = [-0.019, 0.018], p = .951)). In both cases, therefore, the only association in
271   which the error bars did not overlap with zero was with Gradient two.
272
273   Together these analyses revealed that the multivariate effect for the 'problem-solving' item is
274   most clearly positively associated with gradient two while the multivariate effect for the 'past'
275   item shows the reverse pattern. To understand these associations, we visualised the average
276   map of gradient two for individuals in the top and bottom third of similarity with the group-level
277   description, and also calculated the difference. This data is presented in the left-hand panel of
278   Figure 4 where it can be seen that individuals with higher similarity to group-averaged gradient
279   two showed decreased shared connectivity between the visual and sensorimotor systems.
280
281   To visualise the associations between the 'problem-solving' and 'past' questionnaire items
282   with gradient two, we calculated the unique variance associated with gradient two and both
283   questionnaire items separately. To do this, we calculated the residual variance linked to both
284   types of thoughts using linear regressions in which the dependent variable was gradient two
285   similarity scores and the explanatory variables were all of the questionnaire items (as well as
286   age, gender and mean movement) except for the relevant item (either 'problem-solving' or
287   'past'). We performed a comparable analysis to identify the residual variance in gradient two.
288   Together this data is presented in the right-hand panel of Figure 4 where it can be seen that
289   individuals with high similarity scores for gradient two reported more problem-solving thoughts
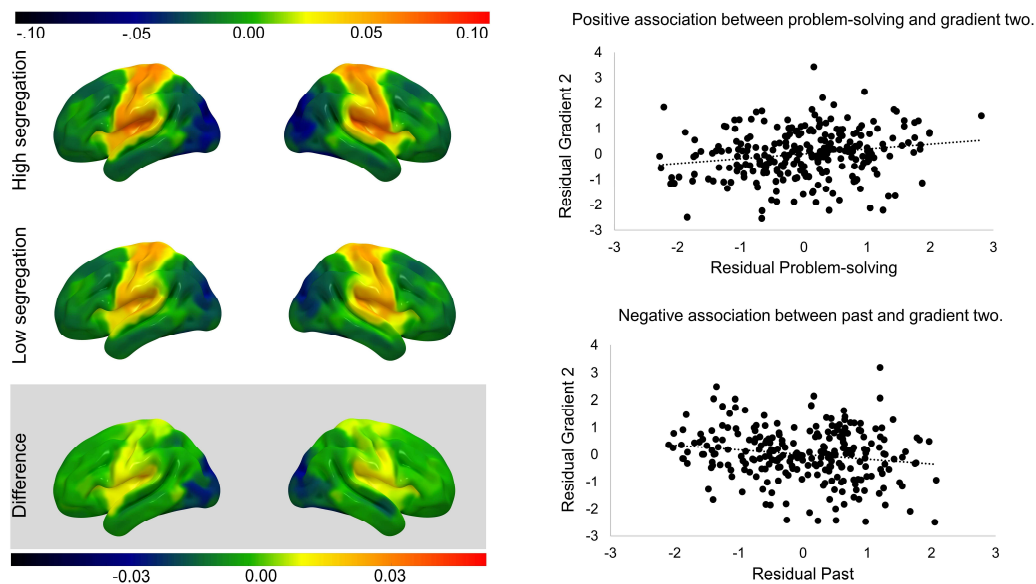290   and fewer past-related thoughts.

291

Figure 4. *Greater functional segregation between visual and sensorimotor cortices was positively associated with reports of problem-solving thoughts during rest and negatively associated with reports of thoughts about past events*. Left panel: group-averaged maps for high (top) and low (middle) similarity scores for gradient two as well as the difference between these groups (bottom). The top colour bar reflects the scale of the high and low similarity group-averaged maps while the bottom colour bar reflects the scale of the difference map. Individuals with high similarity scores showed more functional segregation between visual (blue) and sensorimotor cortices (orange). The proximity of colours reflects greater similarity in connectivity patterns between regions. Right panel (upper): Scatterplot of residuals describing the positive relationship between gradient two similarity and the 'problem-solving' questionnaire item. Each point is a participant. Right panel (lower): Scatterplot of residuals describing the negative relationship between gradient two similarity and the 'past' questionnaire item. Using raw scores, a Pearson correlation confirmed this negative the positive association with problem solving thoughts (r(252) = .16, p = .013) and a negative relationship with past related thoughts (r(252) = -.13, p = .040).

4 Discussion

The current study employed a data-driven approach to identify whole-brain connectivity patterns associated with distinct patterns of ongoing thought at rest. Specifically, we were interested in identifying whether three reasonably well-described macroscale patterns of neural function ('cortical gradients') were related to the experiences an individual had at rest. Participants completed a rs-fMRI scan followed by an experience-sampling questionnaire

313   retrospectively assessing the content and form of their ongoing thoughts during the scan. To

314   reduce the dimensional structure of the rs-fMRI data we used a non-linear dimension reduction

315   algorithm to embed the functional connectivity in a low-dimensional space. We found that

316   individuals with less similarity between the pattern of functional connectivity in visual and

317   sensorimotor cortices were more likely to report thoughts related to finding solutions to

318   problems or goals and less likely to report thoughts related to past events (as demonstrated

319   in figure 4).

320

321   It is worth considering the relationship between the current results and previous findings

322   reported by Karapanagiotidis et al. (2019). They used the same dataset as the current study

323   and applied Hidden Markov modelling to identify neural states. This analysis found two states

324   which were associated with measures of experience. One state was linked to patterns of

325   autobiographical planning (future-oriented problem-solving) and was associated with the

326   dominance of the motor system relative to the visual system. In contrast, a second state was

327   linked to intrusive rumination about the past and exhibited reasonably similar levels of activity

328   in both the visual and motor systems. There is therefore an encouraging correspondence

329   between the results of the current analysis, which entails a decomposition of the resting-state

330   data into low dimensional manifolds, and the prior analyses which identifies neural states

331   which reoccur at rest.

332

333   Together, these results add to a growing body of evidence that suggest neural processing in

334   either primary motor or visual cortex may play an important role in aspects of higher-order

335   cognition, especially those that involve imagining events other than those in the immediate

336   environment. For example, Medea and colleagues asked participants to complete two writing

337   sessions in which they either wrote about three personal goals or three TV programmes

338   (Medea et al., 2018). Before and after each writing session participants completed an

339   experience-sampling session. They found that if participants reported future-directed thought

340   between writing session one and two, the concreteness of their personal goals increased

341   between sessions. Importantly, this pattern was most pronounced for individuals who showed

342   stronger connectivity between the hippocampus and a region of motor cortex at rest.

343   Consistent with the possibility that motor cortex activity can be important during periods of

344   self-generated thought, Sormaz and colleagues used online experience-sampling and found

345   that neural patterns in regions of motor cortex were able to differentiate between thoughts

346   related to a working memory task and those related to personal concerns about the future

347   (Sormaz et al., 2018). Matheson and Kenett (2020) propose that the motor system is likely to

348   be important in creative problem solving because of the capacity for this system to model the

349   simulation of possible actions. Future work will be needed to understand the precise role that
350   motor cortex activity plays in different patterns of ongoing thought.

351

352   There is also converging evidence from fMRI studies suggests that primary visual cortex is
353   recruited during internal processing independent from external stimuli (Muckli, 2010). For
354   example, activity in visual cortex has been observed during the retention period of a working
355   memory task in which no external stimulus was presented (Harrison & Tong, 2009), while
356   Japardi et al., (2018) found that visual system connectivity was important during periods of
357   creativity for visual artists. Furthermore, Villena-Gonzalez et al. (2018) found that the degree
358   of connectivity between the visual cortex and regions of posterior medial cortex were
359   associated with a tendency to employ social information when engaged in task-based
360   prospection. Together with these prior studies, the current work provides converging evidence
361   linking processes in unimodal cortex to aspects of imaginative thought, an important question
362   for future work to explore.

363

364   More generally our data suggests that different aspects of ongoing thought may vary in the
365   degree to which unimodal systems are integrated. Mesulam (1998) argued that if a cortical
366   system only contained unimodal regions, it would have difficulties in performing cognitive acts
367   that depended on regularities that spanned multiple modalities. The connectivity pattern
368   identified in gradient two recapitulates this theoretical functional organization proposed by
369   Mesulam; the relative segregation of the unimodal systems coupled with common connectivity
370   with transmodal and integrative systems such as the default mode network (See figure 5 for a
371   schematic of this architecture). It is possible that the degree of integration between these
372   unimodal systems may help encode and retrieve visual and auditory features of an experience,
373   a process for which regions in the medial temporal lobe such as the hippocampus (Moscovitch
374   et al., 2016) or the anterior temporal lobe (Ralph et al., 2017) may be particularly important.
375   Based on our data we hypothesise that different types of experience may vary with the degree
376   of overlap between these primary systems. Plausibly, a focus on thoughts relating to the past
377   can rely on co-recruitment in both visual and motor regions because these experiences can
378   capitalise on pre-existing memory traces and which may have been particularly strongly
379   encoded if they spontaneously come to mind in a fluent fashion. In contrast, when attempting
380   to generate a novel solution to a problem, it is less easy to capitalise directly on whole-brain
381   associations from the past. Problem solving, therefore, may depend to a greater extent on
382   processes that simulate the specific sequence of actions that should be performed, or, the
383   arrangement of specific features of the environment, and which may be relatively achievable
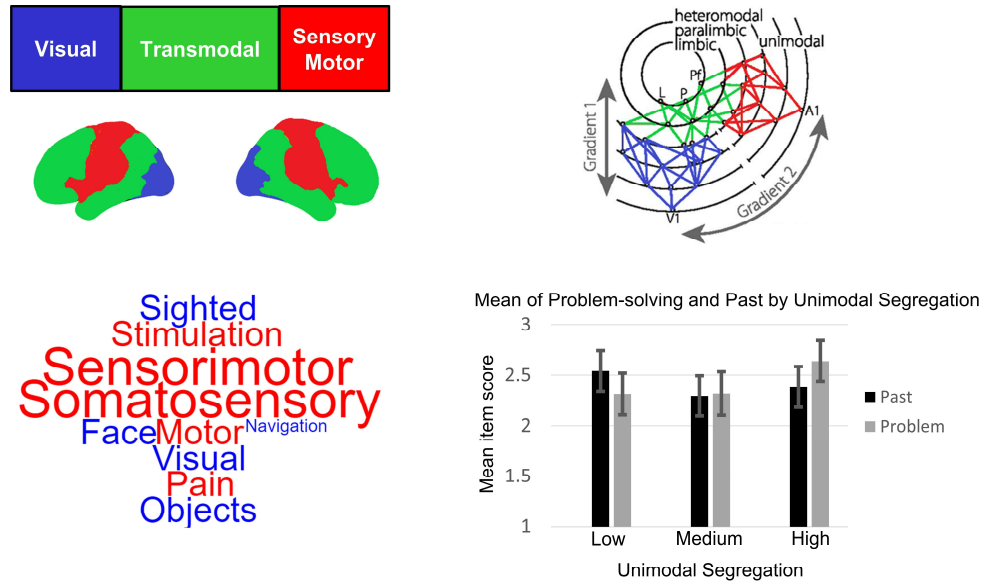384   without interactions across different forms of unimodal cortex.

385

386

387 **Figure 5.** *Schematic of a hypothesised relationship between the macroscale organization and*
388 *patterns of thought with different features.* Left panel (top): Simplified schematic of gradient
389 two representing the segregation of unimodal systems with intermediary transmodal regions
390 in between. Left panel (bottom): Word clouds representing the Neurosynth terms associated
391 with the positive (red) and negative (blue) end of gradient two demonstrating the differences
392 in function in the different unimodal systems. Font size represents the magnitude of the
393 relationship, while the colour illustrates the associated system (blue = visual and red =
394 sensorimotor). Right panel (top): Modified illustration of Mesulam's (1998) proposal of how the
395 cortex is organised according to a functional hierarchy of processing from distinct unimodal
396 systems to integrative transmodal regions. Gradient 1 and 2 labels correspond to the results
397 reported in Margulies et al. (2016). Right panel (bottom): Schematic illustration of how
398 unimodal segregation and integration may be differentially associated with distinct aspects of
399 experience. We divided individuals into low, medium and high groups based on the similarity
400 between visual and sensorimotor systems and plotted the mean scores for problem-solving
401 and past related thoughts. It can be seen that based on our data individuals showing less
402 segregation between unimodal systems reported more thoughts about past events and fewer
403 problem-solving thoughts (and vice versa). Error bars indicate the 95% confidence intervals.

404

405 Finally, the current results lend further support to the view that it is necessary for researchers
406 to distinguish between distinct types of ongoing thought (Seli et al., 2018). Our study shows
407 that different types of ongoing thought are differentially associated with macroscale
408 connectivity patterns, suggesting that different types of ongoing thought are supported by

409 related but distinct mechanisms. Previously, many researchers have conflated various types
410 of ongoing thought under one unitary measure (e.g. Mason et al., 2007; Smallwood et al.,
411 2008). The current results suggest that in doing so, researchers may have made erroneous
412 conclusions regarding the neural correlates of states that may often be discussed together
413 under broad umbrella concepts such as 'mind-wandering'. Accordingly, our results
414 demonstrate the value of the family-resemblances view of mental states which stresses the
415 importance of operationalizing and describing the specific type of experience under
416 investigation (Seli et al., 2018).

417

418 Although our study highlights a relationship between the macroscale organization of neural
419 function at rest and concurrent patterns of ongoing experience, it nonetheless leaves several
420 important questions unanswered. First, the present study focused on assessing static rather
421 than dynamic functional connectivity and so cannot address important features of the
422 relationship between neural dynamics and experience (Kucyi, 2018; Lurie et al., 2018). The
423 choice of static functional connectivity coupled with retrospective sampling at the end of the
424 scan means that the current study is unable to identify neuro-experiential associations that
425 are highly transient and dynamic. One way to extend the current findings could be to
426 incorporate sliding window analysis which consists of calculating a given functional
427 connectivity measure (e.g. correlation) over consecutive windowed sections of data and to
428 measure experience on multiple occasions. This method results in a time series of functional
429 connectivity values which can then be used to assess the temporal fluctuations in functional
430 connectivity within a scanning session (Hutchison et al., 2013). Future work combining
431 gradient analyses with dynamic functional connectivity techniques such as Hidden Markov
432 modelling (Vidaurre et al., 2018) or time-varying multi-network approaches (Betzel & Bassett,
433 2017) with multiple online experience-sampling measures, could help understand how
434 macroscale connectivity patterns and ongoing thought patterns fluctuate together over time.

435

436 While retrospective sampling was chosen in the current study to allow neural dynamics to
437 unfold in a relatively natural way over the scan period (Smallwood & Schooler, 2015), this
438 method is not without its limitations which are important to consider when interpreting the
439 current results. For example, retrospective sampling, compared to online sampling, relies
440 more heavily on the participant's ability to remember their own thoughts. This introduces a
441 number of potential confounds such as participants only reporting their most salient thoughts
442 over the scanning period or some participants being more able than others to accurately recall
443 their own thoughts. However, it is important to note that with more frequent sampling of
444 ongoing experience the time series upon which cortical gradients are calculated would be
445 shortened and this could temper the reliability of these metrics as indicators of neural function

446 (Hong et al., 2020). Another limitation of the current study is that there was no experimental
447 manipulation, making the causal link between macroscale patterns of neural activity and
448 ongoing thoughts unclear. This issue could be fruitfully explored by priming participants to
449 think about finding solutions to problems or goals and observe the changes in ongoing neural
450 connectivity, or through the use of techniques such as trans-magnetic stimulation to disrupt
451 either visual or motor cortex and observe the subsequent changes in patterns of ongoing
452 thought.
453
454 Finally, it is important to note that it is not necessarily the case that the absence of
455 associations with the majority of the items in this battery indicates that these aspects of
456 experience are unimportant at rest. It is possible that other types of neural metric that focus
457 on local patterns are important (such as fractional amplitude of low-frequency fluctuations
458 [fALFF] or regional homogeneity [ReHo]; for example, see Gorgolewski et al., 2014) and that
459 these types of relationship would be missed by our current analytic approach which focused
460 on macroscale patterns of neural organization. It is also possible that other features of
461 analysis are more state-like and detecting these types of patterns would require the capacity
462 to measure both ongoing experience and neural experience across several time points (see
463 Vatansever et al., 2020 for an exploration of this question). Finally, although resting-state is
464 a common method for acquiring brain data and one in which patterns of ongoing experience
465 are important, it is also possible that other contexts provoke different types of experience (for
466 example see Ho et al., 2020). Thus, while our study shows that patterns of problem solving
467 and past related experience are likely to be important aspects of a participants experiences
468 at rest, in the future it will be important to carefully determine the most appropriate items for
469 efficiently describing different features of experience in different situations and examining
470 their relationships to a range of different metrics of static and dynamic neural function.

471 ## 5 Conclusions

472 The current study investigated whether individual variation in ongoing thought patterns is
473 associated with low-dimensional representations of macroscale functional connectivity at rest.
474 Results revealed that reports of thoughts about finding solutions to problems was linked to
475 greater segregation between the visual and sensorimotor systems, while thoughts about past
476 events was linked to less segregation. These associations suggest that the degree of
477 segregation of unimodal systems determine important features of ongoing experience. Future
478 work could investigate the extent to which priming individuals to think about particular topics
479 changes patterns of ongoing neural activity, or, use neurostimulation techniques to alter neural
480 activity and examine how this changes ongoing experience. Such studies would provide

481 important causal evidence on the relationship between macroscale patterns of neural activity
482 and patterns of ongoing thought. Moving forward, it is likely to be increasingly important for
483 scientists studying patterns of functional connectivity in states such as rest, or even tasks to
484 acquire measures of ongoing experience in order to fully appreciate the significance of neural
485 motifs that are revealed through the application of advanced analysis methods. Likewise, it
486 will be important for researchers studying patterns of ongoing thought to recognise that these
487 states are sometimes encoded in complex distributed whole-brain pattern of neural activity,
488 and are not always localizable to a specific modular region of cortex.

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7   Role of funding source

8   Declarations of interest

497 None

498 # 9 Supplementary materials

Scree plot of the scaled eigenvalues of the group-averaged gradients.
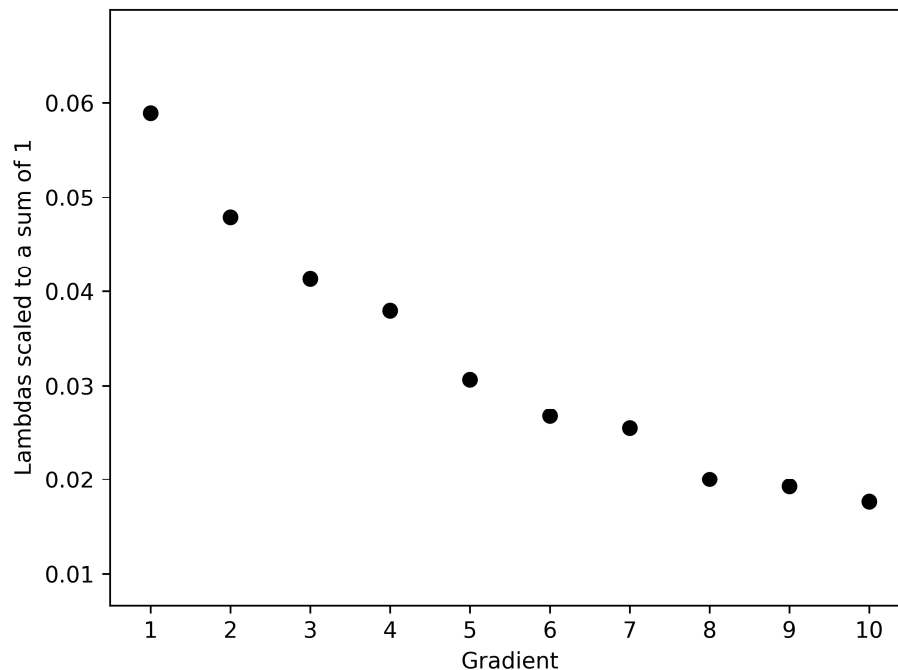
499 **Inline Figure S1.** *Scree plot showing the proportion of variance explained by each of the*
500 *group-averaged whole-brain connectivity gradients one to ten.* Y-axis shows the eigenvalues
501 scaled to a sum of 1. X-axis shows the gradient number. The first three gradients were retained
502 for further multivariate analyses as these gradients have the clearest mapping to cognitive
503 function (e.g. Murphy et al., 2018, 2019; Turnbull et al., in press).

	Unaligned to HCP data	Aligned to HCP data
Gradient 1		
Gradient 2		
Gradient 3		

-.10   -.05   0.00   0.05   0.10
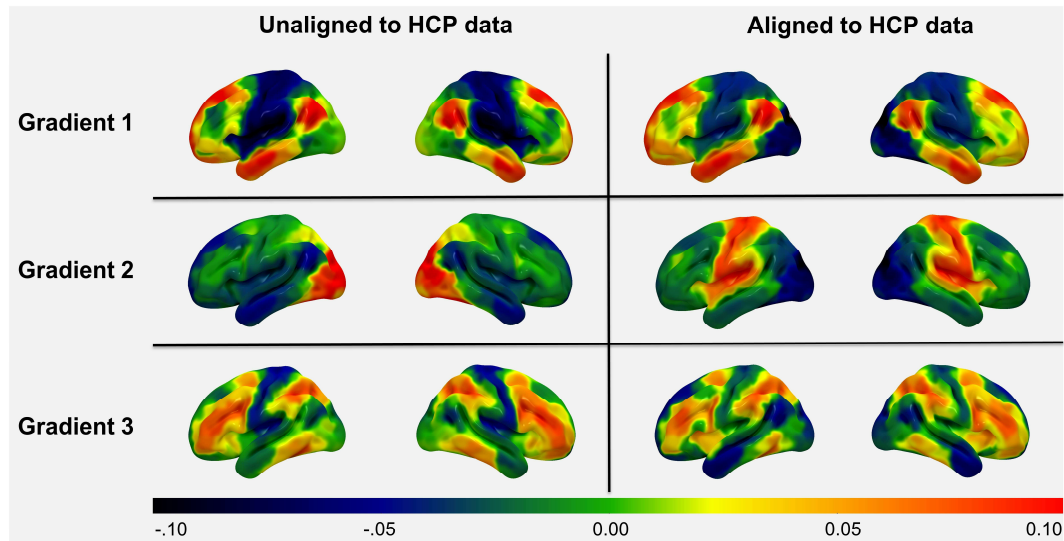
504   **Inline Figure S2.** *Demonstration of how aligning the group-level gradients to a subsample of*
505   *the HCP dataset using Procrustes rotation changes the first three group-level gradients.*
506   Regions that share similar connectivity profiles fall together along each gradient (similar
507   colours) and regions that have more distinct connectivity profiles fall further apart (different
508   colours). It is important to note that the positive and negative loading is arbitrary and can flip
509   each time the diffusion embedding is applied to the data. For example, in this figure, the visual
510   cortex along gradient two has a positive loading in the unaligned map but has a negative
511   loading in the aligned map. Thus, differences in loadings are not meaningful and occur
512   randomly.
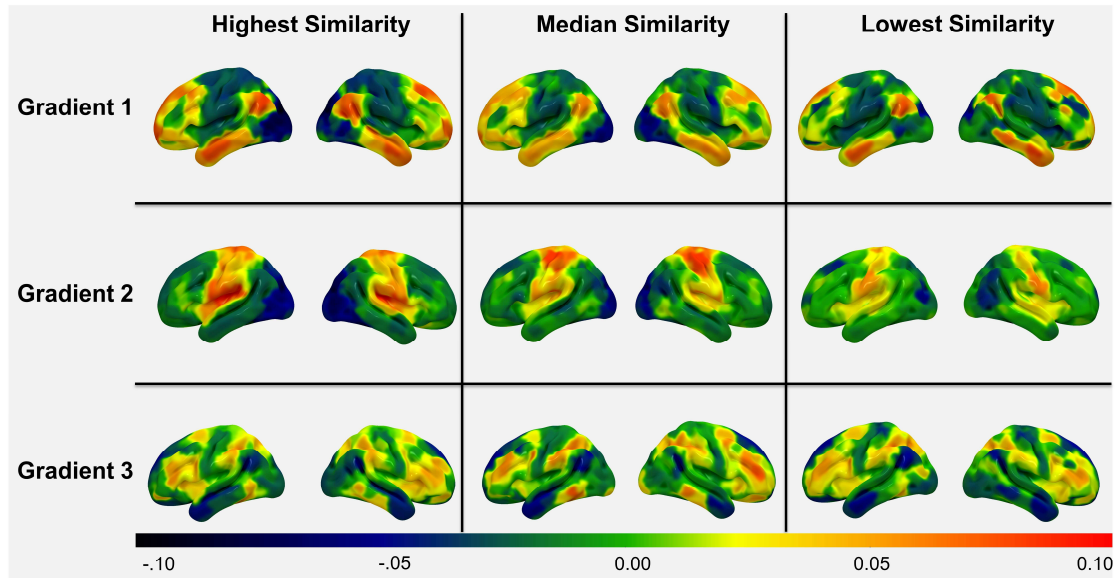
Inline Figure S3. *Individual-level connectivity gradients one to three which have the highest (left), median (middle) and lowest (right) similarity with the respective group-level gradients to demonstrate the variability of gradients across participants in the current sample.* Regions that share similar connectivity profiles fall together along each gradient (similar colours) and regions that have more distinct connectivity profiles fall further apart (different colours). The positive and negative loading is arbitrary.

520

Inline Supplementary Table 1. This table shows the improvement in the degree of fit (or similarity) between individual-level and group-level gradients when extracting ten gradients compared to only extracting three gradients. Mean similarity was calculated by averaging all participant's R-to-Z transformed Spearman Rank correlation coefficients for each respective gradient.				
Extracting 3 gradients:	**Minimum**	**Maximum**	**Mean**	**Std. Deviation**
Gradient 1	0.31	1.31	0.84	0.21
Gradient 2	0.28	1.48	0.84	0.25
Gradient 3	-0.07	1.04	0.57	0.19
Extracting 10 gradients:	**Minimum**	**Maximum**	**Mean**	**Std. Deviation**
Gradient 1	0.7	1.76	1.36	0.16
Gradient 2	0.9	1.85	1.37	0.16
Gradient 3	0.58	1.38	1.12	0.12

521

522

	Aligned to HCP	Unaligned to HCP
Inline Supplementary Table 2. Spearman rank correlation values for the first five aligned and unaligned group-level gradients with the first five group-level gradients reported in Margulies et al (2016). This demonstrates that aligning the group-level gradients to the subsample of HCP data improves correspondence between the gradients calculated in the current study and previous literature.		
Gradient 1	0.62	0.4
Gradient 2	-0.47	0.23
Gradient 3	-0.45	-0.38
Gradient 4	-0.2	0.07
Gradient 5	-0.18	-0.03

523

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