1 **Social belonging: Brain structure and function is linked to membership in sports**
2 **teams, religious groups and social clubs**
3
4 Carolin Kieckhaefer[1], Leonhard Schilbach[1,2], Danilo Bzdok[3,4,5]
5
6 [1] LVR Klinikum Düsseldorf / Department of Psychiatry and Psychotherapy, Heinrich-Heine-
7 University, Düsseldorf, Germany
8 [2] Ludwig Maximilians University, Munich, Germany
9 [3] Montreal Neurological Institute (MNI), McConnell Brain Imaging Centre, Faculty of
10 Medicine and Health Sciences, McGill University, Montreal, Quebec, Canada
11 [4] Department of Biomedical Engineering, Faculty of Medicine and Health Sciences, McGill
12 University, Montreal, Quebec, Canada
13 [5] Mila - Quebec Artificial Intelligence Institute, Montreal, Quebec, Canada
14
15
16 **Abstract**
17 Human behaviour across the life span is driven by the psychological need to belong,
18 from kindergarten to bingo nights. Being part of social groups constitutes a backbone
19 for communal life, and confers many benefits for physical and mental health.
20 Capitalizing on neuroimaging and behavioural data from ~40.000 participants from the
21 UK Biobank population cohort, we used structural and functional analyses to explore
22 how social participation is reflected in the human brain. Across three different types of
23 social groups, structural analyses point towards variance in ventromedial prefrontal
24 cortex, fusiform gyrus and anterior cingulate cortex as structural substrates tightly
25 linked to social participation. Functional connectivity analyses emphasized the
26 importance of default mode and limbic network, but also showed differences for sports
27 teams and religious groups as compared to social clubs.
28 Taken together, our findings establish the structural and functional integrity of the
29 default mode network as a neural signature of social belonging.
30
31
32 **Keywords**: population neuroscience, social deprivation, social capital, Bayesian
33 hierarchical modeling
34
35

Introduction

Belonging to social groups is an indispensable ingredient of everyday life, providing well-documented benefits for mental health and well-being. Regular engagement in social groups of varying complexity has been structuring societies for thousands of years. Experiencing the team spirit in a vibrant soccer match, enjoying a beer in a bar with like-minded persons or resting in collective silent prayer - these are formative experiences that scaffold human social life. These group events are some of many examples of social participation.

The definition of social participation has taken many forms in previous work. Yet, a content analysis revealed the "involvement in activities that provide interactions with others" as a key recurring theme (Levasseur, Richard, et al., 2010). In contrast, the type of activity or level of involvement with the group are more variable. Social participation is associated with enhanced subjective and objective health outcomes (Leone & Hessel, 2016; Sirven & Debrand, 2008), reduction of depressive symptoms (Chiao et al., 2011) and improved overall quality of life (Lestari et al., 2021; Levasseur, Desrosiers, et al., 2010). A representative population-based study in the US showed lower levels of self-rated physical health for people who experience social disconnectedness and perceived isolation (Cornwell & Waite, 2009). The central relevance of social participation was also underscored by the WHO in the context of aging and rehabilitation (WHO, 2002), finding its way into political programs and recommendations aiming to improve global health in disadvantaged populations (Francés et al., 2016). The recent European health policy framework *Health 2020* emphasized participation as a core principle for health equity and well-being (Boyce & Brown, 2017).

The close links between social participation and well-being holds across the life span and is not limited to aging. A transnational study investigated 1047 participants with an average age of 35.5 years from Europe, North-Africa, Western Asia and the Americas in terms of mental health in a period of pandemic-related restrictions on social relations (Ammar et al., 2020). A decrease of social participation due to these restrictions took a negative toll on life satisfaction. Comparing Italian, American and Iranian students, a different study showed positive associations between social participation and well-being, largely mediated by the sense of community (Cicognani et al., 2008). The concept of social participation is closely related to sense of community, sharing several positive effects on individual and social life (Talò et al., 2014).

The sense of community emphasizes the aspect of shared emotional connection of a membership in a community or group. This aspect might be an important explanatory factor of the high social gain in relationships within groups in the periphery of one´s social network. Resulting feelings of connectedness with others in conjunction with social participation was recently discussed as a buffer for less decline in well-being in the sense of a resource (Sharifian & Grühn, 2019). Belonging to a group helps to increase self-acceptance, thus being an important factor in coping processes, especially in challenging situations (Thoits, 2011). Furthermore, the sense of belonging directly and persistently contributes to people's resilience (Scarf et al., 2016).

A further concept that is closely linked to resilience is the sense of meaning and purpose in life. It denotes the skills and readiness for mastering difficult circumstances (Feldman, 2020). A recent study links the association between social interaction and meaning in life to the brain (Mwilambwe-Tshilobo et al., 2019). These authors reported an increased functional connectivity between the default and limbic networks to be associated with a greater sense of life meaning. The increase of perceived meaning in

85 life was repeatedly associated with social participation and belonging to others (Adams
86 et al., 2011; Sharifian & Grühn, 2019). Hence, current limitations of social contacts are
87 a challenge for purposeful living.
88 In the context of the COVID-19 pandemic with widespread loneliness and reduced
89 possibilities of participation due external circumstances, individual resilience gains
90 relevance from a public health standpoint. Being able to cope with and quickly recover
91 from a disaster is critically dependent on active belonging to a group within the
92 resilience process (Quinn et al., 2020). A closer look at the biological manifestations of
93 social belonging and participation at the population-level is imperative, especially as
94 COVID-19 challenged not only regions or communities but affected entire populations.
95 Such confronted life events and overcome obstacles are important to be investigated
96 for the angle of psychopathology and clinical symptoms.
97 In the present population-based approach, we shift the focus towards factors that are
98 known to be key for successful resilience and mental well-being. Regarding how a
99 particular individual handles stressors, previous studies underlined the association
100 between the experience of control as well as resilient coping and the activation of the
101 medial prefrontal cortex (Maier & Watkins, 2010; Sinha et al., 2016). Neuroimaging
102 data from real-life contexts offers important insight into social belonging and its many
103 wide-ranging consequences. One way to understand the broader link between social
104 interactions and its influence on brain architecture has been proposed by the social
105 brain hypothesis. The intensified need and intricacy of social relationships in humans
106 may have spurred refinement towards more complex representation of social bonds in
107 the brain (Dunbar, 2009). Brain systems that have long been described to be closely
108 implicated in social cognition processes involve the default mode network (DMN; Mars
109 et al., 2012). However, based on previous works, the neural basis of social participation
110 and belonging remain obscure. Taken together no human brain-imaging assessments
111 of participation in different group contexts exist, in part because such characteristics of
112 people's everyday social life have seldom been systematically acquired before the
113 emergence of large population datasets such as the UK Biobank cohort. Combining
114 structural and functional neuroimaging as well as demographic profiling with a
115 population-based approach, we investigated three particular forms of social
116 participation: sports teams, religious groups and social clubs. Using a population
117 cohort to examine and understand systematic variations of social belonging and
118 resilience help inform public-health decision making, which ultimately can foster
119 implementation and even interventions in practice.
120
121
122 **Materials and Methods**
123 *Data resources*
124 The UK Biobank is a prospective epidemiology resource that offers extensive
125 behavioural and demographic assessments, medical and cognitive measures, as well
126 as biological samples in a cohort of ~500,000 participants recruited from across Great
127 Britain (https://www.ukbiobank.ac.uk/). This openly accessible population dataset aims
128 to provide multimodal brain-imaging for ~100,000 individuals, planned for completion
129 in 2022. The present study was based on the recent data release from February/March
130 2020 that augmented brain scanning information to ~40,000 participants.
131 In an attempt to improve comparability and reproducibility, our study built on the
132 uniform data preprocessing pipelines designed and carried out by FMRIB, Oxford
133 University, UK (Alfaro-Almagro et al., 2018). We involved data from the ~40,000

participant release with brain-imaging measures of grey matter morphology (T1-weighted MRI [sMRI]) and neural activity fluctuations (resting-state functional MRI [fMRI]) from 48% men and 52% women, aged 40-69 years when recruited (mean age 54.9, standard deviation [SD] 7.5 years). Our study focused on regular social engagement as captured by membership in social group (Bzdok & Dunbar, 2020; Hawkley et al., 2003; Luhmann & Hawkley, 2016). This self-reported item was based on the following question: "Which of the following do you attend once a week or more often?" (data field 6160). Our study focussed on three target groups: people reporting engagement in sports teams, religious groups and social clubs.

Similar measures are found in widely used assessments of social embeddedness (Cohen & Hoberman, 1983; Cyranowski et al., 2013; Hawkley et al., 2005). Conceptually similar (Cyranowski et al. 2013) are also contained in other standard measurement-tools of social embeddedness, such as the Revised UCLA Loneliness Scale (Hawkley et al. 2005) and the Interpersonal Support Evaluation List (Cohen and Hoberman 1983). A variety of studies showed single-item measures of social traits to be reliable and valid (Atroszko et al., 2015; Dollinger & Malmquist, 2009; Mashek et al., 2007). Previous research has used such individual items for successfully measuring social support (Atroszko et al. 2015), community connectedness (Mashek et al. 2007), and perceived social isolation (Ong et al., 2016). For example, the separate item "There are people I can talk to" correlates very highly (r = .88) with the specific dimension of the R-UCLA Loneliness Scale that corresponds to the objective frequency of social interaction (Hawkley et al. 2005).

The present analyses were conducted under UK Biobank application number 25163. All participants provided informed consent. Further information on the consent procedure can be found elsewhere (http://biobank.ctsu.ox.ac.uk/crystal/field.cgi?id=200).

Multimodal brain-imaging and preprocessing procedures

Magnetic resonance imaging scanners (3T MRI Siemens Skyra) were matched at several dedicated imaging sites with the same acquisition protocols and standard Siemens 32-channel radiofrequency receiver head coils. To protect the anonymity of the study participants, brain-imaging data were defaced and any sensitive meta-information was removed. Automated processing and quality control pipelines were deployed (Alfaro-Almagro et al., 2018; Miller et al., 2016). To improve homogeneity of the imaging data, noise was removed by means of 190 sensitivity features. This approach allowed for the reliable identification and exclusion of problematic brain scans, such as due to excessive head motion.

Structural MRI: The sMRI data were acquired as high-resolution T1-weighted images of brain anatomy using a 3D MPRAGE sequence at 1 mm isotropic resolution. Preprocessing included gradient distortion correction (GDC), field of view reduction using the Brain Extraction Tool (Smith, 2002) and FLIRT (Jenkinson et al., 2002; Jenkinson & Smith, 2001), as well as non-linear registration to MNI152 standard space at 1 mm resolution using FNIRT (Andersson et al., 2007). To avoid unnecessary interpolation, all image transformations were estimated, combined and applied by a single interpolation step. Tissue-type segmentation into cerebrospinal fluid (CSF), grey matter (GM) and white matter (WM) was applied using FAST (FMRIB's Automated Segmentation Tool, (Zhang et al., 2001) to generate full bias-field-corrected images. SIENAX (Smith et al., 2002), in turn, was used to derive volumetric measures normalized for head sizes.

183 *Functional MRI:* The fMRI data of intrinsic neural activity were acquired without
184 engagement in a predefined experimental task context at 2.4 mm spatial resolution,
185 time to repeat=0.735s, and with multiband acceleration of 8. A single-band reference
186 image with higher between-tissue contrast and without T1-saturation effects was
187 acquired within the same geometry as the time series of neural activity maps. The
188 reference scan was used for the alignment to other brain-imaging modalities and
189 correction for head motion. Preprocessing was performed using MELODIC (Beckmann
190 & Smith, 2004), including EPI and GDC unwarping, motion correction, grand-mean
191 intensity normalization, and high-pass temporal filtering (Gaussian-weighted least-
192 squares straight line fitting, sigma=50s). The ensuing images were submitted to motion
193 correction using MCFLIRT (Jenkinson et al. 2002). Structured artefacts were removed
194 by combining ICA and FMRIB's ICA-based X-noiseifier (Griffanti et al., 2014). To help
195 reduce unnecessary interpolation effects, all intermediate warp operations were
196 merged into a composite transformation allowing for simultaneous application to fMRI
197 maps. For the display of results (see Figures 1-3), maps were projected to the cortical
198 surface. This was done via volume-to-surface mapping in wb_command
199 (www.humanconnectome.org), based on the Human Connectome Project (HCP)
200 group average template "S1200_MSMAll".
201
202 *Analysis of associations between social participation and grey matter patterns*
203 Neurobiologically interpretable measures of grey matter volume were extracted in all
204 participants by summarizing whole-brain sMRI maps in Montreal Neurological Institute
205 (MNI) reference space. This feature generation step was guided by the topographical
206 brain region definitions of the widely used Schaefer-Yeo atlas comprising 100 parcels
207 (Schaefer et al. 2018). The participant-level brain region volumes provided the input
208 variables for our Bayesian hierarchical modeling approach (cf. below). As a data-
209 cleaning step, inter-individual variation in brain region volumes that could be explained
210 by variables of no interest were regressed out: body mass index, head size, average
211 head motion during task-related brain scans, average head motion during task-
212 unrelated brain scans, head position and receiver coil in the scanner (x, y, and z),
213 position of scanner table, as well as the data acquisition site.
214 To examine population variation of our atlas regions in the context of regular social
215 participation, we have purpose-designed a Bayesian hierarchical model, building on
216 our previous research (Bzdok et al., 2017; Bzdok et al., 2020; Kiesow et al., 2020). In
217 contrast, classical linear regression combined with statistical significance testing would
218 simply have provided p-values against the null hypothesis of no difference between
219 individuals with high and low social participation in each brain region. Instead of limiting
220 our results and conclusions to strict categorical statements, each region being either
221 relevant for differences in social participation or not, our analytical strategy aimed at
222 full probability distributions that expose how brain region volumes converge or diverge
223 in their relation to social participation as evidenced in the UK Biobank population. In a
224 mathematically rigorous way, our approach estimated coherent, continuous estimates
225 of uncertainty for each model parameter at play for its relevance in social participation.
226 Our study thus addressed the question "How certain are we that a regional brain
227 volume is divergent between high and low social participation individuals?". Our
228 analysis did not ask "Is there a strict categorical difference in region volume between
229 high and low social participation individuals?".
230 The elected Bayesian hierarchical framework also enabled simultaneous modeling of
231 multiple organizational principles: i) *segregation* into separate brain regions and ii)

232 *integration* of groups of brain regions in form of spatially distributed brain networks.
233 Two regions of the same atlas network are more likely to exhibit similar volume effects
234 than two regions belonging to two separate brain networks. Each of the region
235 definitions was pre-assigned to one of the 7 large-scale network definitions in the
236 Schaefer-Yeo atlas (Schaefer et al. 2018) or the collection of subcortical regions from
237 the Harvard-Oxford atlas (Desikan et al., 2006), providing a native multilevel structure.
238 Setting up a hierarchical generative process enabled our analytical approach to borrow
239 statistical strength between model parameters at the higher network level and model
240 parameters at the lower level of constituent brain regions. By virtue of exploiting partial
241 pooling, the brain region parameters were modeled themselves by the hyper-
242 parameters of the hierarchical regression as a function of the network hierarchy to
243 explain social participation. Assigning informative priors centered around zero provided
244 an additional form of regularization by shrinking coefficients to zero in the absence of
245 evidence to the contrary. We could thus provide fully probabilistic answers to questions
246 about the morphological relevance of individual brain locations and distributed cortical
247 networks by a joint varying-effects estimation that profited from several biologically
248 meaningful sources of population variation.
249 The model specification placed emphasis on careful inference of unique posterior
250 distributions of parameters at the brain network level to discriminate individuals with
251 (encoded as outcome 0) and without (outcome 1) a certain social group membership:

252

253
$$y \sim Bernoulli(p)$$
254
$$logit(p) = x_1 * \beta_{region_1} + \dots + x_p * \beta_{region_p} +$$
255
$$\alpha_{men[sex]} + \alpha_{women[sex]} + \alpha_{men\_age[sex]} * age_{men} + \alpha_{women\_age[sex]} * age_{women}$$

256

257
$$\beta_{region_{network\_Visual}} \sim MVNormal\left(\begin{bmatrix} 0 \\ \vdots \\ 0 \end{bmatrix}, \Sigma_{Visual}\right); \Sigma_{Visual} = \begin{bmatrix} \sigma_o^2 & \cdots & \\ \vdots & \ddots & \vdots \\ & \cdots & \sigma_o^2 \end{bmatrix}$$

258
$$\beta_{region_{netwok\_SomMot}} \sim MVNormal\left(\begin{bmatrix} 0 \\ \vdots \\ 0 \end{bmatrix}, \Sigma_{SomMot}\right); \Sigma_{SomMot} = \begin{bmatrix} \sigma_p^2 & \cdots & \\ \vdots & \ddots & \vdots \\ & \cdots & \sigma_p^2 \end{bmatrix}$$

259
$$\beta_{region_{network\_Limbic}} \sim MVNormal\left(\begin{bmatrix} 0 \\ \vdots \\ 0 \end{bmatrix}, \Sigma_{Limbic}\right); \Sigma_{Limbic} = \begin{bmatrix} \sigma_q^2 & \cdots & \\ \vdots & \ddots & \vdots \\ & \cdots & \sigma_q^2 \end{bmatrix}$$

260
$$\beta_{region_{network\_Salience}} \sim MVNormal\left(\begin{bmatrix} 0 \\ \vdots \\ 0 \end{bmatrix}, \Sigma_{Salience}\right); \Sigma_{Salience} = \begin{bmatrix} \sigma_r^2 & \cdots & \\ \vdots & \ddots & \vdots \\ & \cdots & \sigma_r^2 \end{bmatrix}$$

261
$$\beta_{region_{network\_Control}} \sim MVNormal\left(\begin{bmatrix} 0 \\ \vdots \\ 0 \end{bmatrix}, \Sigma_{Control}\right); \Sigma_{Control} = \begin{bmatrix} \sigma_s^2 & \cdots & \\ \vdots & \ddots & \vdots \\ & \cdots & \sigma_s^2 \end{bmatrix}$$

262
$$\beta_{region_{network\_DorsalAttn}} \sim MVNormal\left(\begin{bmatrix} 0 \\ \vdots \\ 0 \end{bmatrix}, \Sigma_{DorsalAttn}\right); \Sigma_{DorsalAttn} = \begin{bmatrix} \sigma_t^2 & \cdots & \\ \vdots & \ddots & \vdots \\ & \cdots & \sigma_t^2 \end{bmatrix}$$

263
$$\beta_{region_{network\_Default}} \sim MVNormal\left(\begin{bmatrix} 0 \\ \vdots \\ 0 \end{bmatrix}, \Sigma_{Default}\right); \Sigma_{Default} = \begin{bmatrix} \sigma_u^2 & \cdots & \\ \vdots & \ddots & \vdots \\ & \cdots & \sigma_u^2 \end{bmatrix}$$

264

$$\alpha_{men} \sim \mathcal{N}(0, 1)$$
$$\alpha_{women} \sim \mathcal{N}(0, 1)$$
$$\alpha_{men\_age} \sim \mathcal{N}(0, 1)$$
$$\alpha_{women\_age} \sim \mathcal{N}(0, 1)$$

where *sigma* parameters estimated the overall variance across the *p* brain regions that belong to a given atlas network, independent of whether the volume effects of the respective constituent brain regions had positive or negative direction. As such, the network variance parameters *sigma* directly quantified the magnitude of intra-network coefficients, and thus the overall relevance of a given network in explaining regular social participation based on the dependent region morphology measures. All regions belonging to the same brain network shared the same variance parameter in the diagonal of the covariance matrix, while off-diagonal covariance relationships were zero.

Probabilistic posterior distributions for all model parameters were estimated for the hierarchical models. Our Bayesian approach could thus simultaneously appreciate grey matter variation in segregated brain regions as well as in integrative brain networks in a population cohort. The approximation of the posterior distributions was carried out by the NUTS sampler (Gelman et al., 2014), a type of Markov chain Monte Carlo (MCMC), using the PyMC3 software suite (Salvatier et al., 2016). After tuning the sampler for 4,000 steps, we drew 1,000 samples from the joint posterior distribution over the full set of parameters in the model for analysis. Proper convergence was assessed by ensuring Rhat measures (Gelman et al. 2014) stayed below 1.02.

Analysis of associations between social participation and functional connectivity patterns

Quantitative measures of functional connectivity were computed for cortex-wide brain regions as defined by the Schaefer-Yeo atlas (Schaefer et al. 2018). Functional connectivity profiles for each participant were derived by computing Pearson's correlation between their neural activity fluctuations. To this end, in each participant, the time series of whole-brain fMRI signals, obtained in the absence of an externally structured experimental task, were summarized by averaging for each brain region in the atlas. The approach yielded the functional coupling signature of the whole cortex as a 100 x 100 region coupling matrix for each participant. The ensuing region-region coupling estimates underwent standardization across participants by centering to zero mean and unit scaling to a variance of one (cf. next step). Inter-individual variation in the functional coupling strengths between brain regions that could be explained by variables of no interest were regressed out in a data-cleaning step (analogous to sMRI analysis): body mass index, head size, average head motion during task-related brain scans, average head motion during task-unrelated brain scans, head position as well as receiver coil in the scanner (x, y, and z), position of scanner table, and data acquisition site, as well as age, sex and age-sex interactions.

We then sought the dominant coupling regime – signature or "mode" of population covariation – that provides insight into how functional variability in 100 brain regions can explain regular social participation. Partial least squares (PLS) was an ideal analytical method to decompose the obtained 100 x 100 fingerprint matrix of functional couplings with respect to social participation. The variable set *X* was constructed from the lower triangle of the participants' functional coupling matrices. The target vector *y* encoded more socially engaged participants as +1 and participants without a given

314 social group membership as -1. PLS involves finding the matrix factorization into k low-
315 rank brain representations that maximize the correspondence with our social trait of
316 interest. PLS thus identified the matrix projection that offered the maximal covariance
317 between sets of region couplings in the context of participant reports of social
318 participation.
319 In other words, the extracted functional coupling mode identified the driving linear
320 combinations of cortical brain connections that featured the best correspondence to
321 regular social participation. Concretely, positive (negative) modulation weights
322 revealed increased (decreased) correlation strengths, relative to average functional
323 coupling. This is because the computed functional connectivity estimates were initially
324 normalized to zero mean and unit variance across participants. For example, a
325 functional connectivity input into PLS of 0 denoted the average functional coupling
326 strength in our UK Biobank sample, rather than an absence of functional connectivity
327 between the region pair. The derived pattern of PLS weights, or canonical vectors, thus
328 indicated deviations from average functional coupling variation in our cohort. Moreover,
329 the variable sets were entered into PLS after a confound-removal procedure (cf.
330 above).
331 Next, we assessed the statistical robustness of the resulting dominant PLS mode of
332 functional coupling deviations related to social participation in a non-parametric
333 permutation procedure, following previous research (Miller et al. 2016). Relying on
334 minimal modeling assumptions, a valid empirical null distribution was derived for the
335 Pearson's correlation between low-rank projections of the dominant mode resulting
336 from PLS analysis. In 1,000 permutation iterations, the functional connectivity matrix
337 was held constant, while the social participation labels were submitted to random
338 shuffling. The constructed surrogate datasets preserved the statistical structure
339 idiosyncratic to the fMRI signals, yet permitted to selectively destroy the signal
340 properties that are related to social participation (Efron, 2012). The generated
341 distribution of the test statistic reflected the null hypothesis of random association
342 between the brain's functional coupling and regular social participation across
343 participants. We recorded the Pearson's correlations rho between the perturbed low-
344 rank projections in each iteration. P-value computation was based on the 1,000
345 Pearson's rho estimates from the null PLS model.
346
347 *Demographic profiling analysis of the brain correlates of social participation*
348 We finally performed a profiling analysis of the brain regions that were most strongly
349 associated with regular social participation. Based on our results in brain structure, we
350 carried out a rigorous test for multivariate associations between our top regions and a
351 diverse set of indicators that exemplify the domains of a) basic demographics, b)
352 personality features, c) substance-use behaviours, and d) social network properties
353 (for details see https://www.ukbiobank.ac.uk/data-showcase/). The set of behavioural
354 variables and the set of brain measures were z-scored across participants to conform
355 to zero mean and unit variance. The brain variables were submitted to the top 10
356 (sMRI) of brain measures that were identified as most important in the context of social
357 participation (cf. above). In the case of brain structure, the target brain regions were
358 selected based on the (absolute) modes of the Bayesian posteriors of marginal
359 parameter distributions at the region level (cf. above). In the case of brain function, the
360 target brain connections were selected based the (absolute) effect sizes from the
361 dominant PLS mode (cf. above).

362 Using the two variable sets of brain and behaviour measurements, we then carried out
363 a bootstrap difference analysis of the collection of target traits in individuals with high
364 versus low social participation (Efron & Tibshirani, 1994). In 1,000 bootstrap iterations,
365 we randomly pulled equally sized participant samples to perform a canonical
366 correlation analysis (CCA), in parallel, in individuals with and without social group
367 membership (Miller et al., 2016; Wang et al., 2020). In each resampling iteration, this
368 approach estimated the doubly multivariate correspondence between the brain and
369 behaviour indicators in each group. The ensuing canonical vectors of the dominant
370 CCA mode indicated the most explanatory demographic associations in a given pull of
371 participants. To directly estimate resample-to-resample effects in group differences,
372 the canonical vectors of behavioural rankings were subtracted elementwise between
373 participants from both groups, recorded, and ultimately aggregated across the 1,000
374 bootstrap datasets.
375 This analytical tactic allowed propagating the noise of participant sampling variation
376 into the computed uncertainty estimates of group differences in the UK Biobank cohort.
377 Statistically defensible behavioural dimensions were determined by whether the (two-
378 sided) bootstrap confidence interval included zero or not in the 5/95% bootstrap
379 population interval. In a fully multivariate setting, this non-parametric modeling scheme
380 directly quantified the statistical uncertainty of how a UK Biobank trait is differentially
381 linked to brain-behaviour correspondence as a function of regular social participation.
382
383

384 **Results**
385 We have mined the UK Biobank resource with a focus on social participation that
386 indicate weekly attendance in a sports team, religious group or social club. Brain region
387 information on structural volume and functional coupling was extracted in ~40,000 UK
388 Biobank Imaging participants guided by the Schaefer-Yeo reference atlas (Schaefer et
389 al., 2018). All results have adjusted the brain features for variation that could be
390 explained by age and sex/gender (cf. methods).
391

392 *Structural brain correlates of sports team participation*
393 At the network level, in participants who attend sports teams at least once every week,
394 the highest explanatory relevance across spatially distributed brain regions emerged
395 in the visual network (posterior sigma = 0.08; 10-90% highest posterior density [HPD]
396 = 0.05/0.10), followed by the DMN (sigma = 0.05, HPD = 0.04/0.07) and the limbic
397 network (sigma = 0.05, HPD = 0.01/0.08). Further volume associations for sports team
398 members were located to (in descending order, based on the explanatory quality): the
399 salience network (sigma = 0.05, HPD = 0.02/0.07), frontoparietal control network
400 (sigma = 0.05, HPD = 0.01/0.07), somatomotor network (sigma = 0.03, HPD =
401 0.01/0.05) and dorsal attention network (sigma = 0.02, HPD = 0.01/0.04). Overall, the
402 largest but most uncertain brain-behaviour association was featured by the limbic
403 network. In contrast, as indicated by the narrowness of the inferred network-level
404 posterior parameter distribution, the network with the most certain contribution to
405 explaining volume variation in the context of sports team membership was the DMN
406 (Fig. 1).
407 At the region level of the obtained Bayesian hierarchical modeling solution, positive
408 volume effects emerged especially in the left lingual gyrus (posterior mean = 0.05, 10-
409 90% HPD = 0.01/0.10), right posterior cingulate cortex (mean = 0.08, HPD =
410 0.03/0.14), left middle temporal gyrus (mean = 0.09, HPD = 0.04/0.14), left middle

411   frontal   gyrus   (LH_Default_PFC_6;   mean   =   0.05,   HPD   =   0.01/0.08   and
412   LH_Default_PFC_7; mean = 0.07, HPD = 0.03/0.11) and right parahippocampal gyrus
413   (mean = 0.09, HPD = 0.03/0.16). Negative associations between volume of brain
414   regions and sports team membership were found for the left (mean = -0.10, 10-90%
415   HPD = -0.14/-0.05) and right inferior occipital gyrus (mean = -0.06, HPD = -0.11/-0.01),
416   left lingual gyrus (mean = -0.09, HPD = -0.13/-0.04), left middle occipital gyrus (mean
417   = -0.10, HPD = -0.16/-0.05), left middle temporal gyrus (mean = -0.08, HPD = -0.13/-
418   0.03), left (mean = -0.05, HPD = -0.10/-0.01) and right superior frontal gyrus (mean =
419   -0.09, HPD = -0.14/-0.01), as well as right superior temporal gyrus (mean = -0.06, HPD
420   = -0.11/-0.01). Overall, we found regions of the default and limbic network as well as
421   lingual gyrus, prefrontal and temporal cortex to be the key brain correlates linked to
422   weekly engagement in a sports team.

Structural brain correlations of religious group participation

425   At the network level, for people who attend religious groups on a weekly basis, we
426   found the strongest association between regular social participation and volume
427   variation for the limbic network (posterior sigma = 0.15, 10-90% HPD = 0.05/0.21),
428   somatomotor network (sigma = 0.09, HPD = 0.05/0.11) and the DMN (sigma = 0.07,
429   HPD = 0.05/0.09). In descending order of explanatory quality, the frontoparietal control
430   network (sigma = 0.06, HPD = 0.03/0.09) and salience network (sigma = 0.06, HPD =
431   0.03/0.09) showed relevant effects, accompanied by dorsal attention network (sigma
432   = 0.05, HPD = 0.02/0.07) and visual network (sigma = 0.04, HPD = 0.02/0.07). Similar
433   to our hierarchical pattern analysis on sports teams (cf. above), the prominent effect
434   with greatest uncertainty was seen in the limbic network, while the most certain
435   network-level volume effect was located to the DMN.
436   Regarding region-level effects of the obtained Bayesian hierarchical modeling solution,
437   we identified several relevant regions that characterize regular attendees of religious
438   groups. Positive volume effects became apparent in the left postcentral gyrus
439   (posterior   mean   =   0.10,   10-90%   HPD   =   0.02/0.17),   left   precentral   gyrus
440   (LH_SomMot_4; mean = 0.14, HPD = 0.07/0.20; LH_Default_Temp_1; mean = 0.11,
441   HPD = 0.03/0.18), right precentral gyrus (mean = 0.06, HPD = 0.01/0.12), right middle
442   temporal gyrus (mean = 0.08, HPD = 0.01/0.14), right superior temporal gyrus (mean
443   = 0.10, HPD = 0.03/0.16) and right rostral anterior cingulate cortex (mean = 0.09, HPD
444   = 0.02/0.16). Furthermore, we identified a set of regions that showed a negative
445   association with religious group participation: left inferior parietal lobule (mean = -0.08,
446   HPD = -0.13/-0.01), left inferior frontal gyrus (mean = -0.07, HPD = -0.13/-0.01), right
447   paracentral lobule (mean = -0.07, HPD = -0.13/-0.01), right dorsal anterior cingulate
448   cortex (mean = -0.16, HPD = -0.26/-0.06) and right inferior frontal gyrus (mean = -0.09,
449   HPD = -0.15/-0.03). As such, similar to our results for sports team members (cf. above),
450   the default and limbic network were highlighted in spiritually active people.

Structural brain correlates of social club participation

453   At the network level, social participation in the form of weekly attendance of social
454   clubs was also linked to a collection of grey matter deviations of atlas region sets. In
455   this third and last analysis of social participation, the largest explained variance and
456   also the most uncertain effect was found for the limbic network (posterior sigma = 0.15,
457   10-90% HPD = 0.05/0.20). The following networks were less explanatory (in
458   descending order): the visual network (sigma = 0.08, HPD = 0.05/0.10), salience
459   network (sigma = 0.06, HPD = 0.03/0.09), somatomotor network (sigma = 0.05, HPD

460 = 0.02/0.08), dorsal attention network (sigma = 0.05, HPD = 0.02/0.07), DMN (sigma
461 = 0.04, HPD = 0.01/0.06) and control network (sigma = 0.03, HPD = 0.01/0.05). The
462 most informative distribution among the seven networks for social club attendance is
463 the visual network, followed closely by the default network.
464 At the region-level of the obtained Bayesian hierarchical modeling solution, we found
465 volume effects characterizing social club members for the atlas region sets. A positive
466 effect for grey matter volume was found for the left (posterior mean = 0.07, 10-90%
467 HPD = 0.01/0.13) and right parahippocampal gyrus (mean = 0.11, HPD = 0.04/0.19),
468 left inferior temporal gyrus (mean = 0.11, HPD = 0.05/0.17), right fusiform gyrus (mean
469 = 0.11, HPD = 0.04/0.17), right cuneus (mean = 0.09, HPD = 0.03/0.14) and right
470 anterior cingulate cortex (mean = 0.11, HPD = 0.03/0.19). We identified the most
471 relevant negative volume deviations for social club participants in the left lingual gyrus
472 (mean = -0.06, HPD = -0.11/-0.01), left precentral gyrus (mean = -0.06, HPD = -0.11/-
473 0.01), left dorsal and ventral anterior cingulate cortex (mean = -0.11, HPD = -0.18/-
474 0.04), right lingual gyrus (mean = -0.10, HPD = -0.15/-0.03) and right middle temporal
475 gyrus (mean = -0.13, HPD = -0.22/-0.04). In agreement with our findings for sports
476 team and religious group members, regions of the limbic and default network were
477 again found to be prominent (Table 1). In addition, among all three groups, similar
478 regions tended to come to the fore, including parahippocampal and fusiform gyrus,
479 anterior cingulate cortex, temporal and prefrontal cortex (Fig. 2).

481 *Functional brain correlates of social participation*
482 Next, fMRI data from our UK Biobank cohort were examined to investigate possible
483 deviations in functional coupling fingerprints related to weekly engagement in sports
484 teams, religious groups and social clubs. The cortex-wide functional connectivity
485 profiles of each participant were submitted to a multivariate pattern-learning algorithm
486 that identified a collection of reliable positive and negative shifts in network connectivity
487 in the context of social participation ($p < 0.05$). In so doing, the single most coherent
488 pattern of deviation for the functional connectome of participants within each of the
489 three groups was identified (Fig. 3).
490 The regular attendees of sports teams showed wide-ranging deviations in intra-
491 network connectivity of default and limbic network. The somatomotor network revealed
492 negative coupling effects in intra-network connectivity. An increase in inter-network
493 connectivity was dominated by connections from the DMN, but also featured the limbic
494 and frontoparietal control network's functional ties to the somatomotor network.
495 Strengthened coupling was detected between the DMN and most other examined
496 large-scale functional networks, including visual network, somatomotor network,
497 frontoparietal control network and limbic network. The frontoparietal control network
498 was found to exhibit enhanced coupling links especially with both the visual and
499 somatomotor networks. A decrease in functional coupling strength was observed for
500 the somatomotor network, the visual network and the dorsal attention network.
501 People participating in religious groups in turn were especially characterized by a
502 compounding of within-network functional connections within the DMN, limbic network
503 and to some extent also in the frontoparietal control network. These three neural
504 network systems showed enhanced within- and between-network functional
505 connectivity patterns. In contrast, the dorsal attention network and the visual network
506 both showed reduced within-network connectivity strengths. Connectivity strengths
507 between regions of the DMN and the neural circuits of the limbic, frontoparietal control
508 and dorsal attention network were significantly increased. Furthermore, we identified a

509 decrease in connectivity strengths between the visual network and several other large-
510 scale networks, including dorsal attention network, frontoparietal control network,
511 salience network as well as the somatomotor network to a reduced extent.
512 In contrast to these two types of social participation, social participation in social clubs
513 did not lead to a salient increase of functional connectivity strengths within most of the
514 aforementioned networks. Instead, a relevant decrease in functional connectivity was
515 noted within DMN and limbic networks as the single most coherent pattern of deviation.
516 The DMN in turn showed enhanced functional coupling with the somatomotor and the
517 dorsal attention networks.
518 As such, among all three types of social participation, the default and the limbic network
519 stuck out in the overall collection of observed deviations in region-region coupling
520 strengths. This insight was evidenced by enhanced connectivity patterns in active
521 members of sports teams and religious groups, and by diminished connectivity
522 patterns in social club participants. Additionally, reminiscent of our general findings
523 from the structural analyses (cf. above), the default and limbic network played a
524 prominent role among the systematic shifts of between-network coupling.
525
526 *Demographic profiling analyses of social participation*
527 In the final set of analyses, we have linked grey matter volume deviation in the most
528 relevant identified regions (top 10%) to behavioural and sociodemographic data via a
529 multivariate pattern analysis in each of the three groups of social participation (Fig. 4).
530 In terms of consistent findings across groups, the time spent watching television ranked
531 highest in all three separate analyses: sports teams (mean = -0.39, 5/95% confidence
532 interval [CI] = -0.90/-0.07), religious groups (mean = -0.44, CI = -0.73/-0.08) and social
533 clubs (mean = -0.56, CI = -0.93/-0.16). Another of our findings that were broadly
534 consistent across all three groups pertained to the number of persons in the closest
535 family circle: the number of siblings, brothers and sisters, showed high concordance
536 across members of sports teams (mean$_{sisters}$ = -0.20, 5/95% CI = -0.66/0.10;
537 mean$_{brothers}$ = -0.16, CI = -0.71/0.15), of religious groups (mean$_{sisters}$ = -0.40, CI = -
538 0.73/0.01; mean$_{brothers}$ = -0.41, CI = -0.77/-0.01) and of social clubs (mean$_{sisters}$ = -0.32,
539 CI = -0.68/0.06; mean$_{brothers}$ = -0.31, CI = -0.66/0.06). Group membership was also
540 reflected by similarities in health-related lifestyle behaviours. Again, all three forms of
541 social participation showed similar convergence for the type and extent of the
542 consumption of alcohol intake (amount of alcohol drunk on a typical drinking day,
543 alcohol intake frequency) and tobacco use (past tobacco smoking, current tobacco
544 smoking). To a varying extent, different psychological conditions also showed a high
545 concordance within all three groups of social participation. These psychological
546 conditions included including loneliness, mood swings, neuroticism, fed-up feelings,
547 suffer from "nerves", tense, miserableness, irritability and sensitivity. In sum, charting
548 relevant brain-behaviour associations revealed a high concordance among all three
549 forms of social participation on sociodemographic and behavioural level for family
550 structure, alcohol and tobacco consumption.
551
552 **Discussion**
553 Experiencing times of unmet social desire and not being able to fulfil one's need to
554 belong can be a wake-up call and highlights the pivotal importance of community and
555 social exchange. Consequently, exploring the neurobiological substrates of social
556 participation and their ties to physical and mental health is imperative. In our present
557 investigation, the DMN and the limbic system were placed in the center of robust brain

558 manifestations across three examined types of social participation in ~40,000 UK
559 Biobank participants: sports teams, religious groups, and social clubs. First, our
560 structural analyses demonstrated the importance of prefrontal and cingulate cortex.
561 Parts of the ventromedial prefrontal cortex (vmPFC) emerged as particularly relevant
562 for participation in all three social groups. Second, in our analyses of functional
563 coupling fingerprints, the DMN and limbic system also emerged consistently among all
564 three groups as the cornerstone of the neural bases indicative of social embeddedness
565 via group membership. Third, the combination of neuroimaging with behavioural and
566 sociodemographic data showed a high consistency among all three types of
567 participation for alcohol and tobacco consumption as well as certain psychological
568 states. Hence, participants of sport teams, religious groups and social clubs do not
569 only show similarities on the neural level, but also on the level of substance use
570 behaviour and mood.

571 The close involvement of the DMN in social and affective processes has been reported
572 on multiple occasions (Amft et al., 2015; Amodio & Frith, 2006; Hyatt et al., 2015; Mars
573 et al., 2012; Redcay & Schilbach, 2019; Schilbach et al., 2008). The relevance of the
574 DMN in subserving advanced social capacities in various contexts has repeatedly been
575 highlighted based on studies of both functional connectivity and grey matter volume
576 (Che et al., 2014; Chen et al., 2010; Finlayson-Short et al., 2020; Lee, 2014; Morita et
577 al., 2021; Takeuchi et al., 2014). Volume variation in the DMN related to social
578 cognition has been reported for the prefrontal cortex as well as the anterior cingulate
579 cortex (Morita et al., 2021) and posterior cingulate cortex (Che et al., 2014). Volume
580 associations with the limbic system were previously linked to the extent of social
581 support and satisfying friendship bonds (Taebi et al., 2020). Extending these previous
582 findings, our present study reveals volume deviation and shifts in functional
583 connectivity patterns that center on the DMN. We linked this neural system to real-
584 world membership in a sports team, religious group or social club on the population
585 level for the first time. This broadens the interpretational perspective on the DMN by
586 adding relevant aspects of everyday life that cannot usually be studied in experimental
587 MRI research.

588 Looking at specific regions related to the DMN, we found that the vmPFC showed a
589 positive volume effect in participants of social clubs and a negative volume effect in
590 participants of sports teams and religious groups. Lesion studies as well as
591 neuroimaging studies in humans and animals pointed out the important role of the
592 vmPFC in complex forms of social cognition, such as mentalization, empathy and
593 decision making (Hiser & Koenigs, 2018; Leopold et al., 2012; Shamay-Tsoory et al.,
594 2003). Larger volume of the vmPFC has been directly linked to the size of an
595 individual's social network and mentalizing competences (Lewis et al., 2011; Powell et
596 al., 2012).

597 The anterior cingulate cortex (ACC) and parahippocampal gyrus are often attributed to
598 the limbic system. The parahippocampal gyrus revealed additional grey matter volume
599 within sports team and social club participants. The ACC showed significant volume
600 deviations for religious groups and social clubs but none for sport teams. For religious
601 groups, ventral parts of ACC showed positive volume effects, while dorsal parts
602 showed negative volume effects. For social club members, dorsal and ventral volume
603 effects for cingulate cortex differed between the two hemispheres. Given that social
604 behaviour is potentially most uniquely developed in the human species (Frith & Frith,
605 2010) it may come as no surprise to find brain asymmetry features, as hemispheric
606 asymmetry is also exceptionally well developed in the human brain (Hartwigsen et al.,

607 2021). The regional findings match the notable interindividual variability of the limbic-
608 trait associations at the network-level of our Bayesian hierarchical analyses. Only
609 recently, grey matter volume increase in the dorsal and perigenual ACC was linked to
610 *social affective benefit* (Gan et al., 2021). The community-based cohort study recorded
611 daily-life social contacts and affective valence via smartphone for one week and
612 combined the data with neuroimaging. Applied to the current results, this might indicate
613 less social affective benefit from the membership in religious groups.
614 The fusiform gyrus is classically associated with processing information from other
615 people's faces. These neural processes assist in recognizing a person identity from
616 their unique facial features – hence, especially stable features of other's faces
617 (Schilbach et al., 2012). The posterior superior temporal sulcus in turn is repeatedly
618 linked to basic sensory input relevant for processing social interactions (right
619 hemisphere; Isik et al., 2017; Walbrin et al., 2018) and also to face processing (Bzdok
620 et al., 2011; Bzdok et al., 2012). Furthermore, this region is classically linked to
621 processing variable facial features like eye gaze and emotional cues.
622 Previous studies compared the neuronal activation of fusiform gyrus and posterior
623 superior temporal sulcus through trustworthiness, attractiveness, emotion and age
624 judgments (Bzdok et al., 2012; Oosterhof & Todorov, 2008). While posterior superior
625 temporal sulcus was associated with trustworthiness judgments, the fusiform gyrus
626 was recruited by attractiveness judgments. In our study we found a volume increase
627 of the fusiform gyrus for participants of sports teams and social clubs, but none for
628 participants of religious group. With respect to the posterior superior temporal sulcus
629 we found volume decrease within the group of sports team attendees and volume
630 increase within attendees of religious groups. This suggests that processing of facial
631 properties of other individuals may be of greater importance in social clubs and sport
632 teams than in religious groups.
633 Those regions with the most pronounced volume deviations in our study have been
634 widely connected to characteristics of social participation such as social network size.
635 A previous functional neuroimaging study with resting-state functional magnetic
636 resonance imaging found a positive association between social network size and the
637 connectivity strength between the amygdala and superior temporal sulcus, as well as
638 that between fusiform gyrus and to vmPFC respectively (Bickart et al., 2012). A related
639 study by Bickert and colleagues (2011) linked the human social network size to brain
640 structure of caudal inferior temporal sulcus, medial frontal cortex and ACC. The
641 number of social contacts within one's online social network (Facebook) has previously
642 been linked to cortical volume deviation in the posterior superior temporal sulcus, as
643 well as middle temporal gyrus (Kanai et al., 2012). Extending these results from human
644 to non-human primates, macaques with a larger social network showed an increase in
645 grey matter volume in rostral prefrontal cortex, ACC and superior temporal sulcus
646 (Sallet et al., 2011). Our analysis regarding social participation highlighted several
647 regions that were mentioned in the context of social network size. This indicates, that
648 social participation is linked to a larger social network.
649 Only recently, the relevance of the DMN in the context of a lack of social connection,
650 in other words loneliness has been highlighted (Spreng et al., 2020). Based on the
651 results in Spreng and colleagues (2020) and those of our study, we can say that
652 overlapping networks are implicated both for social isolation and social participation.
653 Results included similar volume deviations in regions for participants feeling lonely,
654 such ACC, posterior superior temporal sulcus and fusiform gyrus. Even on the network
655 level, the relevance of DMN within lonely participants was alike the results within the

656 groups of social participation. Hence, loneliness and social participation seem to tap
657 on similar brain networks and may even be viewed as opposite ends of a continuum.
658 Besides loneliness as a subjective form of social isolation, social support reflects an
659 objective form of social isolation.
660 Social support is another key construct closely related to social participation. The
661 construct of social support comprises closest friends and family, with a direct impact
662 on health and well-being (Dunbar, 2018). Perhaps counterintuitive at first glance,
663 results for social support and variance in brain regions showed less concordance to
664 our results for social participation (Schurz et al., 2021). Although both assess lifestyle
665 phenotypes that are related to forms of social cognition, only the effect of the limbic
666 network and the volume deviation in the ACC appear to be more closely borne out by
667 our present results. We speculate that the relevance of DMN and limbic system for
668 social participation might derive from two sides. On the one hand, subjective aspects
669 may be rooted in the DMN and reflect components like the sense of belonging to a
670 group, hence less loneliness. Similarly, objective aspects of social participation may
671 be linked to the limbic system and are possibly referring to a larger social network,
672 providing social support.
673 On the conceptual level, social participation is not only used in various ways as a term
674 but also measured in sometimes diverging ways (Chang & Coster, 2014), with
675 constituent aspects consisting of a social role (e.g., daughter/son, friend, club member)
676 and a social task (e.g., work environment, school). To date, the construct of social
677 participation is predominantly discussed in the context of rehabilitation and healthy
678 aging, being extensively investigated as an outcome measure (Douglas et al., 2017;
679 Piškur et al., 2014).
680 As an empirical approach taken by our study, we examined three concrete forms of
681 structured social participation with regular attendance. Sharing the same interest might
682 in part be a consequence of shared personality traits, potentially linked to
683 corresponding neural correlates. In support of this hypotheses, similarity of (autistic)
684 personality traits in friendships of healthy adults was recently shown to be linked to
685 friendship quality (Bolis et al., 2021). Especially as interindividual similarity in
686 personality, social cognition and behaviour promote getting "in sync" and building
687 meaningful social relationships (Hyon et al., 2020; Redcay & Schilbach, 2019).
688 In addition to a number of commonalities in brain structure and function, we also found
689 differences between participants of sports teams, social clubs and religious groups.
690 These differences might depend on the types of regular experienced interaction with
691 the people who tend to be at the periphery of one's social circles. For regular physical
692 activity, positive effects on brain development and cognition in adolescence are
693 presented (Herting & Chu, 2017). Herein reviewed neuroimaging studies reported
694 volume increase in hippocampus and lingual gyrus was related to aerobic training.
695 Improved cognition due to physical activity included executive functions, cognitive
696 flexibility and inhibitory control. A review study attributes an increase in grey matter
697 volume to physical activity for all brain regions except for superior temporal gyrus and
698 fusiform gyrus (Batouli & Saba, 2017). However, in our study we found volume
699 deviation for these two regions in sport team members as well. This in fact may be
700 driven by social aspects of sport participation rather than physical activity.
701 For groups related to religious beliefs and spirituality, altered functional coupling
702 patterns in the DMN have been reported and was discussed in the context of mystical
703 and "insight" experiences (van Elk & Aleman, 2017). Differences in social processing
704 between religious and nonreligious participants were found but controversial discussed

705　at the same time, with special attention to peer influence and membership in religious
706　groups (Grafman et al., 2020). Furthermore, no consistent grey matter volume
707　differences for religiosity and mystical experiences were found in a recent voxel-based
708　morphometry study (van Elk & Snoek, 2020). A meta-analytic study found no positive
709　longevity effects based on individuals' beliefs but still suggests positive health effects
710　from simply belonging to a religious group (Shor & Roelfs, 2013). These effects include
711　health-related behaviours and a sense of comfort and meaning, as the sheer result of
712　social participation.
713　Adolescents with regular participation in different types of social clubs had a healthier
714　lifestyle and protective effect of belonging to at least one club was described
715　(Borraccino et al., 2020; Zambon et al., 2010). Older adults participating in social
716　activities benefit from reduction of stress and improvements in several important
717　dimensions of mental health (Mackenzie & Abdulrazaq, 2021). Another systematic
718　review associated long-term commitment to social activity groups with executive
719　functioning, social network size and global cognition (e.g. memory, executive function;
720　Kelly et al., 2017). The surveyed intervention studies included sport groups (e.g., Tai
721　Chi, walking) and social clubs (e.g., photo group, quilt group).
722　Hence, societies offering more ample opportunities for participation in sports, religious
723　or social activities, not only dampen loneliness and cognitive decline but improve
724　people's resilience and might reduce the risk for dementia. In contrast, loneliness and
725　social isolation are associated with loss of cognitive capacity (Lara et al., 2019), such
726　as measured by Wechsler Adult Intelligence Scale, Consortium to Establish a Registry
727　for Alzheimer´s Disease and digit span test. The previous studies provide various
728　results concerning the impact of the particular nature of the investigated groups.
729　Reported positive effects on health and cognition as well as deviations in brain
730　structures might primarily derive from the recurring engagement with a group per se.
731　In our study, we reported minor differences in brain structure and function among all
732　three examined groups of social participation. However, similarities tended to dominate
733　on structural and functional level in our collective findings.
734　Within our results, convergence was also shown across the different demographic
735　profiling　analyses. These brain-phenotype associations showed high similarity within
736　most factors among participants of sports teams, religious groups and social clubs.
737　Highest overlap across all three groups was observed in the factors television
738　consumption, number of siblings, health-related lifestyle behaviour and psychological
739　conditions. Although the direction of the revealed associations has no single answer in
740　the fully multivariate setting, previous research reported general positive effects of
741　group participation on substance use (Elder et al., 2000). Indeed, a wide range of
742　previous studies presented heterogenous effects of physical activity on increased risk
743　for substance use among adolescents (Murray et al., 2021; Terry-Mcelrath et al.,
744　2011). While the similarity within psychological conditions, health factors and
745　substance-use (limited to tobacco, nicotine, alcohol) is in line with recent findings in
746　people receiving high social support (Schurz et al., 2021), being explained by general
747　health effects of social relations (Holt-Lunstad et al., 2010), watching television and
748　family size stand out. The individual consumption of television of adolescents was
749　associated with the TV consumption of their peer group (Fletcher, 2006). Furthermore,
750　siblings foster social competence, especially in a young age (Downey et al., 2015).
751　More specific, perspective taking can be improved by siblings but findings vary and
752　depend on the family context (Sang & Nelson, 2017). Again, despite of differences in

753 the participated activity, commonalities exceed among the investigated groups in the
754 demographic profiling analyses.
755 Membership to social groups scaffolds human life in society. Extending previous
756 experimental neuroscience evidence, our investigation shows that brain substrates of
757 social participation are interrelated with health-related concepts like social support and
758 psychological well-being at the population level. Among all three examined types of
759 groups, we identified the DMN and limbic network as central for social participation.
760 Both highlighted networks gained further relevance in the context of belonging to a
761 group, as aspects of everyday life participation were studied in a population cohort and
762 could be related to additional demographic and everyday-life information. In a
763 comprehensive demographic profiling analysis, we here find concrete benefits of social
764 participation in groups such as reduced substance use and improved psychological
765 well-being.
766 Overall, our collective findings could be taken to suggest that the concrete type of
767 social participation may be of less importance than the regular attendance itself.
768 Looking for a way to harness the positive effects of social participation, this calls for
769 accessible forms of routine interventions in cohesive social groups, sometimes
770 described as 'social prescribing'. This is all the more important in periods of social
771 isolation in which a lack of social participation takes its toll on mental health.
772
773
774
775 **Acknowledgements**

782
784
785
786

References

Adams, K. B., Leibbrandt, S., & Moon, H. (2011). A critical review of the literature on social and leisure activity and wellbeing in later life. *Ageing and Society*, *31*(4), 683–712. https://doi.org/10.1017/S0144686X10001091

Alfaro-Almagro, F., Jenkinson, M., Bangerter, N. K., Andersson, J. L. R., Griffanti, L., Douaud, G., Sotiropoulos, S. N., Jbabdi, S., Hernandez-Fernandez, M., Vallee, E., Vidaurre, D., Webster, M., McCarthy, P., Rorden, C., Daducci, A., Alexander, D. C., Zhang, H., Dragonu, I., Matthews, P. M., … Smith, S. M. (2018). Image processing and Quality Control for the first 10,000 brain imaging datasets from UK Biobank. *NeuroImage*, *166*, 400–424. https://doi.org/10.1016/j.neuroimage.2017.10.034

Amft, M., Bzdok, D., Laird, A., Fox, P. T., Schilbach, L., & Eickhoff, S. B. (2015). Definition and characterization of an extended social-affective default network. In *Brain Struct Funct* (Vol. 220, Issue 2). https://doi.org/10.1007/springerreference_184020

Ammar, A., Chtourou, H., Boukhris, O., Trabelsi, K., Masmoudi, L., Brach, M., Bouaziz, B., Bentlage, E., How, D., Ahmed, M., Mueller, P., Mueller, N., Hsouna, H., Aloui, A., Hammouda, O., Paineiras-Domingos, L. L., Braakman-Jansen, A., Wrede, C., Bastoni, S., … Hoekelmann, A. (2020). Covid-19 home confinement negatively impacts social participation and life satisfaction: A worldwide multicenter study. *International Journal of Environmental Research and Public Health*, *17*(6237), 1–17. https://doi.org/10.3390/ijerph17176237

Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: The medial frontal cortex and social cognition. *Nature Reviews Neuroscience*, *7*(4), 268–277. https://doi.org/10.1038/nrn1884

Andersson, J., Jenkinson, M., & Smith, S. (2007). *Non-linear registration aka Spatial normalisation FMRIB Technical Report TR07JA2. FMRIB*. Analysis Group of the University of Oxford.

Atroszko, P., Baginska, P., Mokosinska, M., Sawicki, A., & Atroszko, B. (2015). Validity and reliability of single-item self-report measures of general quality of life, general health and sleep quality. *CER Compar Eur Res, 216*.

Batouli, S. A. H., & Saba, V. (2017). At least eighty percent of brain grey matter is modifiable by physical activity: A review study. *Behavioural Brain Research*, *332*(May), 204–217. https://doi.org/10.1016/j.bbr.2017.06.002

Beckmann, C., & Smith, S. (2004). Probabilistic independent component analysis for functional magnetic resonance imaging. *IEEE Trans Med Imaging, 23*, 137–152.

Bickart, K. C., Hollenbeck, M. C., Barrett, L. F., & Dickerson, B. C. (2012). Intrinsic amygdala-cortical functional connectivity predicts social network size in humans. *Journal of Neuroscience*, *32*(42), 14729–14741. https://doi.org/10.1523/JNEUROSCI.1599-12.2012

Bickart, K. C., Wright, C. I., Dautoff, R. J., Dickerson, B. C., & Barrett, L. F. (2011). Amygdala volume and social network size in humans. *Nature Neuroscience*, *14*(2), 163–164. https://doi.org/10.1038/nn.2724

Bolis, D., Lahnakoski, J. M., Seidel, D., Tamm, J., & Schilbach, L. (2021). Interpersonal similarity of autistic traits predicts friendships quality. *Social Cognitive and Affective Neuroscience*, *16*(1–2), 222–231.

Borraccino, A., Lazzeri, G., Kakaa, O., Bad'ura, P., Bottigliengo, D., Dalmasso, P., & Lemma, P. (2020). The contribution of organised leisure-time activities in

836   shaping positive community health practices among 13-and 15-year-old
837   adolescents: Results from the health behaviours in school-aged children study in
838   italy. *International Journal of Environmental Research and Public Health*, *17*(18),
839   1–12. https://doi.org/10.3390/ijerph17186637
840   Boyce, T., & Brown, C. (2017). Engagement and participation for health equity. In
841   *World Health Organization Europe*.
842   http://www.euro.who.int/__data/assets/pdf_file/0005/353066/Engagement-and-
843   Participation-HealthEquity.pdf?ua=1
844   Bzdok, D., Langner, R., Caspers, S., Kurth, F., Habel, U., Zilles, K., Laird, A., &
845   Eickhoff, S. B. (2011). ALE meta-analysis on facial judgments of trustworthiness
846   and attractiveness. *Brain Structure and Function*, *215*(3–4), 209–223.
847   https://doi.org/10.1007/s00429-010-0287-4
848   Bzdok, D, Eickenberg, M., Varoquaux, G., & Thirion, B. (2017). Hierarchical region-
849   network sparsity for high-dimensional inference in brain imaging. *Inf Process*
850   *Med Imaging*, *10265*, 323–335.
851   Bzdok, Danilo, & Dunbar, R. I. M. (2020). The Neurobiology of Social Distance.
852   *Trends in Cognitive Sciences*, *24*(9), 717–733.
853   https://doi.org/10.1016/j.tics.2020.05.016
854   Bzdok, Danilo, Floris, D. L., & Marquand, A. F. (2020). Analysing brain networks in
855   population neuroscience: A case for the Bayesian philosophy. *Philosophical*
856   *Transactions of the Royal Society B: Biological Sciences*, *375*(1796), 1–11.
857   https://doi.org/10.1098/rstb.2019.0661
858   Bzdok, Danilo, Langner, R., Hoffstaedter, F., Turetsky, B. I., Zilles, K., & Eickhoff, S.
859   B. (2012). The modular neuroarchitecture of social judgments on faces. *Cerebral*
860   *Cortex*, *22*(4), 951–961. https://doi.org/10.1093/cercor/bhr166
861   Chang, F. H., & Coster, W. J. (2014). Conceptualizing the construct of participation in
862   adults with disabilities. *Archives of Physical Medicine and Rehabilitation*, *95*(9),
863   1791–1798. https://doi.org/10.1016/j.apmr.2014.05.008
864   Che, X. W., Wei, D. T., Li, W. F., Li, H. J., Qiao, L., Qiu, J., Zhang, Q. L., & Liu, Y. J.
865   (2014). The correlation between gray matter volume and perceived social
866   support: A voxel-based morphometry study. *Social Neuroscience*, *9*(2), 152–159.
867   https://doi.org/10.1080/17470919.2013.873078
868   Chen, A. C., Welsh, R. C., Liberzon, I., & Taylor, S. F. (2010). "Do I like this person?"
869   A network analysis of midline cortex during a social preference task.
870   *NeuroImage*, *51*(2), 930–939. https://doi.org/10.1016/j.neuroimage.2010.02.044
871   Chiao, C., Weng, L. J., & Botticello, A. L. (2011). Social participation reduces
872   depressive symptoms among older adults: An 18-year longitudinal analysis in
873   Taiwan. *BMC Public Health*, *11*. https://doi.org/10.1186/1471-2458-11-292
874   Cicognani, E., Pirini, C., Keyes, C., Joshanloo, M., Rostami, R., & Nosratabadi, M.
875   (2008). Social participation, sense of community and social well being: A study
876   on American, Italian and Iranian University students. *Social Indicators Research*,
877   *89*(1), 97–112. https://doi.org/10.1007/s11205-007-9222-3
878   Cohen, S., & Hoberman, H. M. (1983). Positive Events and Social Supports as
879   Buffers of Life Change Stress. *Journal of Applied Social Psychology*, *13*(2), 99–
880   125.
881   Cornwell, E. Y., & Waite, L. J. (2009). Social disconnectedness, perceived isolation,
882   and health among older adults. *Journal of Health and Social Behavior*, *50*(1),
883   31–48. https://doi.org/10.1177/002214650905000103
884   Cyranowski, J. M., Zill, N., Bode, R., Butt, Z., Kelly, M., Pilkonis, P., Salsman, J., &

Cella, D. (2013). Assessing Social Support, Companionship, and Distress: NIH Toolbox Adult Social Relationship Scales. *Health Psychol*, *32*(3), 293–301. https://doi.org/10.1037/a0028586.Assessing

Desikan, R., Ségonne, F., Fischl, B., Quinn, B., Dickerson, B., Blacker, D., Buckner, R., Dale, A., Maguire, R., & Hyman, BT, et al. (2006). An automated labeling system for subdividing the human cerebral cortex on MRI scans into gyral based regions of interest. *NEUROIMAGE*, *31*, 968–980.

Dollinger, S., & Malmquist, D. (2009). Reliability and validity of single-item self-reports: With special relevance to college students` alcohol use, religiosity, study, and social life. *The Journal of General Psychology*, *136*(3), 231–241.

Douglas, H., Georgiou, A., & Westbrook, J. (2017). Social participation as an indicator of successful aging: An overview of concepts and their associations with health. *Australian Health Review*, *41*(4), 455–462. https://doi.org/10.1071/AH16038

Downey, D. B., Condron, D. J., & Yucel, D. (2015). Number of Siblings and Social Skills Revisited Among American Fifth Graders. *Journal of Family Issues*, *36*(2), 273–296. https://doi.org/10.1177/0192513X13507569

Dunbar, Robin I.M. (2018). The Anatomy of Friendship. *Trends in Cognitive Sciences*, *22*(1), 32–51.

Efron, B. (2012). *Large-scale inference: empirical bayes methods for estimation, testing, and prediction* (p. Cambridge (UK): Cambridge University Press.).

Efron, B., & Tibshirani, R. (1994). *An introduction to the bootstrap*.

Elder, C., Leaver-Dunn, D., Wang, M. Q., Nagy, S., & Green, L. (2000). Organized Group Activity as a Protective Factor Against Adolescent Substance Use. *American Journal of Health Behavior*, *24*(2), 108–113.

Feldman, R. (2020). What is resilience: an affiliative neuroscience approach. *World Psychiatry*, *19*(2), 132–150. https://doi.org/10.1002/wps.20729

Finlayson-Short, L., Davey, C. G., & Harrison, B. J. (2020). Neural correlates of integrated self and social processing. *Social Cognitive and Affective Neuroscience*, 941–949.

Fletcher, J. (2006). Social interactions in adolescent television viewing. *Archives of Pediatrics and Adolescent Medicine*, *160*(4), 383–386. https://doi.org/10.1001/archpedi.160.4.383

Francés, F., La Parra, D., Martínez Asunción, M. R., Ortiz Barreda, G., & Briones Vozmediano, E. (2016). Toolkit on social participation. In *World Health Organization Europe*. https://www.euro.who.int/__data/assets/pdf_file/0003/307452/Toolkit-social-partecipation.pdf

Frith, U., & Frith, C. (2010). The social brain: Allowing humans to boldly go where no other species has been. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1537), 165–175. https://doi.org/10.1098/rstb.2009.0160

Gan, G., Ma, R., Reichert, M., Giurgiu, M., Ebner-Priemer, U. W., Meyer-Lindenberg, A., & Tost, H. (2021). Neural Correlates of Affective Benefit From Real-life Social Contact and Implications for Psychiatric Resilience. *JAMA Psychiatry*, 5–7. https://doi.org/10.1001/jamapsychiatry.2021.0560

Gelman, A., Carlin, J., Stern, H., & Rubin, D. (2014). *Bayesian data analysis. Vol 2*.

Grafman, J., Cristofori, I., Zhong, W., & Bulbulia, J. (2020). The Neural Basis of Religious Cognition. *Current Directions in Psychological Science*, *29*(2), 126–133. https://doi.org/10.1177/0963721419898183

Griffanti, L., Salimi-Khorshidi, G., Beckmann, C., Auerbach, E., Douaud, G., Sexton, C., E, Z., Ebmeier, K., Filippini, N., & Mackay, C. (2014). ICA-based artefact removal and accelerated fMRI acquisition for improved resting state network imaging. *Neuroimage*, *95*, 232–247.

Hartwigsen, G., Bengio, Y., & Bzdok, D. (2021). How does hemispheric specialization contribute to human-defining cognition? *Neuron*, 1–16. https://doi.org/10.1016/j.neuron.2021.04.024

Hawkley, L. C., Browne, M. W., & Cacioppo, J. T. (2005). How can I connect with thee? Let me count the ways. *Psychological Science*, *16*(10), 798–804. https://doi.org/10.1111/j.1467-9280.2005.01617.x

Hawkley, L. C., Burleson, M. H., Berntson, G. G., & Cacioppo, J. T. (2003). Loneliness in Everyday Life: Cardiovascular Activity, Psychosocial Context, and Health Behaviors. *Journal of Personality and Social Psychology*, *85*(1), 105–120. https://doi.org/10.1037/0022-3514.85.1.105

Herting, M. M., & Chu, X. (2017). Exercise, cognition, and the adolescent brain. *Birth Defects Research*, *109*(20), 1672–1679. https://doi.org/10.1002/bdr2.1178

Hiser, J., & Koenigs, M. (2018). The multifaceted role of ventromedial prefrontal cortex in emotion, decision-making, social cognition, and psychopathology. *Biol Psychiatry*, *83*(8), 638–647. https://doi.org/10.1016/j.biopsych.2017.10.030.The

Holt-Lunstad, J., Smith, T. B., & Layton, J. B. (2010). Social relationships and mortality risk: A meta-analytic review. *PLoS Medicine*, *7*(7). https://doi.org/10.1371/journal.pmed.1000316

Hyatt, C. J., Calhoun, V. D., Pearlson, G. D., & Assaf, M. (2015). Specific default mode subnetworks support mentalizing as revealed through opposing network recruitment by social and semantic FMRI tasks. *Human Brain Mapping*, *36*(8), 3047–3063. https://doi.org/10.1002/hbm.22827

Hyon, R., Youm, Y., Kim, J., Chey, J., Kwak, S., & Parkinson, C. (2020). Similarity in functional brain connectivity at rest predicts interpersonal closeness in the social network of an entire village. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(52), 33149–33160. https://doi.org/10.1073/PNAS.2013606117

Isik, L., Koldewyn, K., Beeler, D., & Kanwisher, N. (2017). Perceiving social interactions in the posterior superior temporal sulcus. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(1), E9145–E9152. https://doi.org/10.1073/pnas.1721071115

Jenkinson, M., Bannister, P., Brady, M., & Smith, S. (2002). Improved optimization for the robust and accurate linear registration and motion motion correction of brain images. *NEUROIMAGE*, *17*, 825–841.

Jenkinson, M., & Smith, S. (2001). A global optimisation method for robust affine registration of brain images. *Med Image Anal*, *5*, 143–156.

Kanai, R., Bahrami, B., Roylance, R., & Rees, G. (2012). Online social network size is reflected in human brain structure. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 1327–1334. https://doi.org/10.1098/rspb.2011.1959

Kelly, M. E., Duff, H., Kelly, S., McHugh Power, J. E., Brennan, S., Lawlor, B. A., & Loughrey, D. G. (2017). The impact of social activities, social networks, social support and social relationships on the cognitive functioning of healthy older adults: A systematic review. *Systematic Reviews*, *6*(259). https://doi.org/10.1186/s13643-017-0632-2

Kiesow, H., Dunbar, R., Kable, J., Kalenscher, T., Vogeley, K., Schilbach, L.,

983   Marquand, A., Wiecki, T., & Bzdok, D. (2020). 10,000 social brains: sex
984   differentiation inhuman brain anatomy. *Sci Adv*, *6*(eaaz1170), 1–12.

985 Lamblin, M., Murawski, C., Whittle, S., & Fornito, A. (2017). Social connectedness,
986   mental health and the adolescent brain. *Neuroscience and Biobehavioral*
987   *Reviews*, *80*, 57–68. https://doi.org/10.1016/j.neubiorev.2017.05.010

988 Lara, E., Caballero, F. F., Rico-Uribe, L. A., Olaya, B., Haro, J. M., Ayuso-Mateos, J.
989   L., & Miret, M. (2019). Are loneliness and social isolation associated with
990   cognitive decline? *International Journal of Geriatric Psychiatry*, *34*(11), 1613–
991   1622. https://doi.org/10.1002/gps.5174

992 Law, M. (2002). Participation in the occupations of everyday life. *American Journal of*
993   *Occupational Therapy*, *56*(6), 640–649. https://doi.org/10.5014/ajot.56.6.640

994 Lee, T.-C. (2014). Trilogy of body imaginary: Dance/movement therapy for a
995   psychiatric patient with depression. *Arts in Psychotherapy*, *41*(4), 400–408.
996   https://doi.org/10.1016/j.aip.2014.07.006

997 Leone, T., & Hessel, P. (2016). The effect of social participation on the subjective and
998   objective health status of the over-fifties: Evidence from SHARE. *Ageing and*
999   *Society*, *36*(5), 968–987. https://doi.org/10.1017/S0144686X15000148

1000 Leopold, A., Krueger, F., Dal monte, O., Pardini, M., Pulaski, S. J., Solomon, J., &
1001   Grafman, J. (2012). Damage to the left ventromedial prefrontal cortex impacts
1002   affective theory of mind. *Social Cognitive and Affective Neuroscience*, *7*(8), 871–
1003   880. https://doi.org/10.1093/scan/nsr071

1004 Lestari, S. K., de Luna, X., Eriksson, M., Malmberg, G., & Ng, N. (2021). A
1005   longitudinal study on social support, social participation, and older Europeans'
1006   Quality of life. *SSM - Population Health*, *13*(February).
1007   https://doi.org/10.1016/j.ssmph.2021.100747

1008 Levasseur, M., Desrosiers, J., & Whiteneck, G. (2010). Accomplishment level and
1009   satisfaction with social participation of older adults: Association with quality of life
1010   and best correlates. *Quality of Life Research*, *19*(5), 665–675.
1011   https://doi.org/10.1007/s11136-010-9633-5

1012 Levasseur, M., Richard, L., Gauvin, L., & Raymond, É. (2010). Inventory and analysis
1013   of definitions of social participation found in the aging literature: Proposed
1014   taxonomy of social activities. *Social Science and Medicine*, *71*(12), 2141–2149.
1015   https://doi.org/10.1016/j.socscimed.2010.09.041

1016 Lewis, P. A., Rezaie, R., Brown, R., Roberts, N., & Dunbar, R. I. M. (2011).
1017   Ventromedial prefrontal volume predicts understanding of others and social
1018   network size. *NeuroImage*, *57*(4), 1624–1629.
1019   https://doi.org/10.1016/j.neuroimage.2011.05.030

1020 Luhmann, M., & Hawkley, L. C. (2016). Age Differences in Loneliness from Late
1021   Adolescence to Oldest Old Age. *Dev Psychol*, *52*(6), 943–959.
1022   https://doi.org/10.1037/dev0000117.Age

1023 Mackenzie, C. S., & Abdulrazaq, S. (2021). Social engagement mediates the
1024   relationship between participation in social activities and psychological distress
1025   among older adults. *Aging & Mental Health*, *25*(2), 299–305.

1026 Maier, S. F., & Watkins, L. R. (2010). Role of the medial prefrontal cortex in coping
1027   and resilience. *Brain Research*, *1355*, 52–60.
1028   https://doi.org/10.1016/j.brainres.2010.08.039

1029 Maij, D. L. R., Van Harreveld, F., Gervais, W., Schrag, Y., Mohr, C., & Van Elk, M.
1030   (2017). Mentalizing skills do not differentiate believers from non-believers, but
1031   credibility enhancing displays do. In *PLoS ONE* (Vol. 12, Issue 8).

https://doi.org/10.1371/journal.pone.0182764

Mars, R. B., Neubert, F. X., Noonan, M. A. P., Sallet, J., Toni, I., & Rushworth, M. F. S. (2012). On the relationship between the "default mode network" and the "social brain." *Frontiers in Human Neuroscience, 6*(JUNE 2012), 1–9. https://doi.org/10.3389/fnhum.2012.00189

Mashek, D., Cannaday, L., & Tangney, J. (2007). Inclusion of community in self scale: a single-item pictorial measure of community connectedness. *Journal of Community Psychology, 35*(2), 257–275. https://doi.org/10.1002/jcop

Miller, K. L., Alfaro-Almagro, F., Bangerter, N. K., Thomas, D. L., Yacoub, E., Xu, J., Bartsch, A. J., Jbabdi, S., Sotiropoulos, S. N., Andersson, J. L. R., Griffanti, L., Douaud, G., Okell, T. W., Weale, P., Dragonu, I., Garratt, S., Hudson, S., Collins, R., Jenkinson, M., … Smith, S. M. (2016). Multimodal population brain imaging in the UK Biobank prospective epidemiological study. *Nature Neuroscience, 19*(11), 1523–1536. https://doi.org/10.1038/nn.4393

Morita, T., Asada, M., & Naito, E. (2021). Gray-matter expansion of social brain networks in individuals high in public self-consciousness. *Brain Sciences, 11*(374). https://doi.org/10.3390/brainsci11030374

Murray, R. M., Sabiston, C. M., Doré, I., Bélanger, M., & O'Loughlin, J. L. (2021). Longitudinal associations between team sport participation and substance use in adolescents and young adults. *Addictive Behaviors, 116*, 106798.

Mwilambwe-Tshilobo, L., Ge, T., Chong, M., Ferguson, M. A., Misic, B., Burrow, A. L., Leahy, R. M., & Spreng, R. N. (2019). Loneliness and meaning in life are reflected in the intrinsic network architecture of the brain. *Social Cognitive and Affective Neuroscience, 14*(4), 423–433. https://doi.org/10.1093/scan/nsz021

Ong, A. D., Uchino, B. N., & Wethington, E. (2016). Loneliness and Health in Older Adults: A Mini-Review and Synthesis. *Gerontology, 62*(4), 443–449. https://doi.org/10.1159/000441651

Oosterhof, N. N., & Todorov, A. (2008). The functional basis of face evaluation. *Proceedings of the National Academy of Sciences of the United States of America, 105*(32), 11087–11092. https://doi.org/10.1073/pnas.0805664105

Piškur, B., Daniëls, R., Jongmans, M. J., Ketelaar, M., Smeets, R. J. E. M., Norton, M., & Beurskens, A. J. H. M. (2014). Participation and social participation: Are they distinct concepts? *Clinical Rehabilitation, 28*(3), 211–220. https://doi.org/10.1177/0269215513499029

Powell, J., Lewis, P. A., Roberts, N., García-Fiñana, M., & Dunbar, R. I. M. (2012). Orbital prefrontal cortex volume predicts social network size: An imaging study of individual differences in humans. *Proceedings of the Royal Society B: Biological Sciences, 279*(1736), 2157–2162. https://doi.org/10.1098/rspb.2011.2574

Quinn, T., Adger, W. N., Butler, C., & Walker-Springett, K. (2020). Community resilience and well-being: an exploration of relationality and belonging after disasters. *Annals of the American Association of Geographers, 111*(2), 577–590.

Redcay, E., & Schilbach, L. (2019). *Using second- person neuroscience to elucidate the mechanisms of social interaction. 20*(August), 495–505.

Sallet, J., Mars, R. B., Noonan, M. P., Andersson, J. L., O´Reilly, J. X., Jbabdi, S., Croxson, P. L., Jenkinson, M., Miller, K. L., & Rushworth, M. F. S. (2011). Social Network Size Affects Neural Circuits in Macaques. *Science, 334*(6056), 697–700. https://doi.org/10.4159/harvard.9780674333987.c22

Salvatier, J., Wiecki, T., & Fonnesbeck, C. (2016). Probabilistic programming in python using PyMC3. *PeerJ Computer Science, 2*(e55), 1–24.

1081   Sang, S. A., & Nelson, J. A. (2017). The effect of siblings on children's social skills
1082   and perspective taking. *Infant and Child Development*, *26*(6), 1–10.
1083   https://doi.org/10.1002/icd.2023
1084   Scarf, D., Moradi, S., McGaw, K., Hewitt, J., Hayhurst, J. G., Boyes, M., Ruffman, T.,
1085   & Hunter, J. A. (2016). Somewhere I belong: Long-term increases in
1086   adolescents' resilience are predicted by perceived belonging to the in-group.
1087   *British Journal of Social Psychology*, *55*(3), 588–599.
1088   https://doi.org/10.1111/bjso.12151
1089   Schaefer, A., Kong, R., Gordon, E. M., Laumann, T. O., Zuo, X.-N., Holmes, A. J.,
1090   Eickhoff, S. B., & Yeo, B. T. T. (2018). Local-Global Parcellation of the Human
1091   Cerebral Cortex from Intrinsic Functional Connectivity MRI. *Cerebral Cortex*,
1092   *28*(9), 3095–3114. https://doi.org/10.1093/cercor/bhx179
1093   Schilbach, L., Bzdok, D., Timmermans, B., Fox, P. T., Laird, A. R., Vogeley, K., &
1094   Eickhoff, S. B. (2012). Introspective Minds: Using ALE meta-analyses to study
1095   commonalities in the neural correlates of emotional processing, social &
1096   unconstrained cognition. *PLoS ONE*, *7*(2).
1097   https://doi.org/10.1371/journal.pone.0030920
1098   Schilbach, L., Eickhoff, S. B., Rotarska-Jagiela, A., Fink, G. R., & Vogeley, K. (2008).
1099   Minds at rest? Social cognition as the default mode of cognizing and its putative
1100   relationship to the "default system" of the brain. *Consciousness and Cognition*,
1101   *17*(2), 457–467. https://doi.org/10.1016/j.concog.2008.03.013
1102   Schurz, M., Uddin, L. Q., Kanske, P., Lamm, C., Sallet, J., Bernhardt, B. C., Mars, R.
1103   B., & Bzdok, D. (2021). Variability in Brain Structure and Function Reflects Lack
1104   of Peer Support. *Cerebral Cortex*, 1–16. https://doi.org/10.1093/cercor/bhab109
1105   Shamay-Tsoory, S. G., Tomer, R., Berger, B. D., & Aharon-Peretz, J. (2003).
1106   Characterization of empathy deficits following prefrontal brain damage: The role
1107   of the right ventromedial prefrontal cortex. *Journal of Cognitive Neuroscience*,
1108   *15*(3), 324–337. https://doi.org/10.1162/089892903321593063
1109   Sharifian, N., & Grühn, D. (2019). The Differential Impact of Social Participation and
1110   Social Support on Psychological Well-Being: Evidence From the Wisconsin
1111   Longitudinal Study. *International Journal of Aging and Human Development*,
1112   *88*(2), 107–126. https://doi.org/10.1177/0091415018757213
1113   Shor, E., & Roelfs, D. J. (2013). The longevity effects of religious and nonreligious
1114   participation: A meta-analysis and meta-regression. *Journal for the Scientific
1115   Study of Religion*, *52*(1), 120–145. https://doi.org/10.1111/jssr.12006
1116   Sinha, R., Lacadie, C. M., Constable, R. T., & Seo, D. (2016). Dynamic neural activity
1117   during stress signals resilient coping. *Proceedings of the National Academy of
1118   Sciences of the United States of America*, *113*(31), 8837–8842.
1119   https://doi.org/10.1073/pnas.1600965113
1120   Sirven, N., & Debrand, T. (2008). Social participation and healthy ageing: An
1121   international comparison using SHARE data. *Social Science and Medicine*,
1122   *67*(12), 2017–2026. https://doi.org/10.1016/j.socscimed.2008.09.056
1123   Smith, S. (2002). Fast robust automated brain extraction. *Hum Brain Mapp*, *17*, 143–
1124   155.
1125   Smith, S., Zhang, Y., Jenkinson, M., Chen, J., Matthews, P., Federico, A., & De
1126   Stefano, N. (2002). Accurate, robust, and automated longitudinal and cross-
1127   sectional brain change analysis. *NEUROIMAGE*, *17*, 479–489.
1128   Spreng, R. N., Dimas, E., Mwilambwe-tshilobo, L., Dagher, A., Koellinger, P., Nave,
1129   G., Ong, A., Kernbach, J. M., Wiecki, T. V, Ge, T., Li, Y., Holmes, A. J., Yeo, B.

1130   T. T., Turner, G. R., Dubar, R. I. M., & Bzdok, D. (2020). The default network of
1131   the human brain is associated with perceived social isolation. *Nature*
1132   *Communications*, 1–11. http://dx.doi.org/10.1038/s41467-020-20039-w
1133 Taebi, A., Kiesow, H., Vogeley, K., Schilbach, L., Bernhardt, B. C., & Bzdok, D.
1134   (2020). Population variability in social brain morphology for social support,
1135   household size and friendship satisfaction. *Social Cognitive and Affective*
1136   *Neuroscience*, *15*(6), 635–647. https://doi.org/10.1093/scan/nsaa075
1137 Takeuchi, H., Taki, Y., Sassa, Y., Hashizume, H., Sekiguchi, A., Fukushima, A., &
1138   Kawashima, R. (2014). Regional gray matter volume is associated with
1139   empathizing and systemizing in young adults. *PLoS ONE*, *9*(1).
1140   https://doi.org/10.1371/journal.pone.0084782
1141 Talò, C., Mannarini, T., & Rochira, A. (2014). Sense of Community and Community
1142   Participation: A Meta-Analytic Review. *Social Indicators Research*, *117*(1), 1–28.
1143   https://doi.org/10.1007/s11205-013-0347-2
1144 Terry-Mcelrath, Y. M., O'Malley, P. M., & Johnston, L. D. (2011). Exercise and
1145   substance use among american youth, 1991-2009. *American Journal of*
1146   *Preventive Medicine*, *40*(5), 530–540.
1147   https://doi.org/10.1016/j.amepre.2010.12.021
1148 Thoits, P. A. (2011). Mechanisms linking social ties and support to physical and
1149   mental health. *Journal of Health and Social Behavior*, *52*(2), 145–161.
1150   https://doi.org/10.1177/0022146510395592
1151 van Elk, M., & Aleman, A. (2017). Brain mechanisms in religion and spirituality: An
1152   integrative predictive processing framework. *Neuroscience and Biobehavioral*
1153   *Reviews*, *73*, 359–378. https://doi.org/10.1016/j.neubiorev.2016.12.031
1154 van Elk, M., & Snoek, L. (2020). The relationship between individual differences in
1155   gray matter volume and religiosity and mystical experiences: A preregistered
1156   voxel-based morphometry study. *European Journal of Neuroscience*, *51*(3),
1157   850–865. https://doi.org/10.1111/ejn.14563
1158 Walbrin, J., Downing, P., & Koldewyn, K. (2018). Neural responses to visually
1159   observed social interactions. *Neuropsychologia*, *112*(February), 31–39.
1160   https://doi.org/10.1016/j.neuropsychologia.2018.02.023
1161 Wang, S., Tepfer, L. J., Taren, A. A., & Smith, D. V. (2020). Functional parcellation of
1162   the default mode network: a large-scale meta-analysis. *Scientific Reports*, *10*(1),
1163   1–13. https://doi.org/10.1038/s41598-020-72317-8
1164 WHO (World Health Organization). (2002). Active ageing: a policy framework. In
1165   *Geneva, Switzerland: World Health Organization.*
1166 Zambon, A., Morgan, A., Vereecken, C., Colombini, S., Boyce, W., Mazur, J.,
1167   Lemma, P., & Cavallo, F. (2010). The contribution of club participation to
1168   adolescent health: Evidence from six countries. *Journal of Epidemiology and*
1169   *Community Health*, *64*(1), 89–95. https://doi.org/10.1136/jech.2009.088443
1170 Zhang, Y., Brady, M., & Smith, S. (2001). Segmentation of brain MR images through
1171   a hidden Markov random field model and the expectation-maximization
1172   algorithm. *IEEE Trans Med Imaging*, *20*, 45–57.
1173
1174
1175
1176
1177

Table 1. List of analyzed 7 networks, based on Schaefer-Yeo atlas, in decreasing order of explained variance (top to bottom) based on highest posterior density (HPD).

	Social participation			Social support	Loneliness
	Sports team	Religious group	Social club	(Schurz et al., 2021)	(Spreng et al., 2020)
Decreasing relevance →	visual	**limbic****	**limbic****	salience	**default***
	default*	somatomotor	**visual***	**limbic****	**limbic****
	limbic**	**default***	salience	somatomotor	dorsal attn
	salience	control	somatomotor	dorsal attn	somatomotor
	control	salience	dorsal attn	visual	visual
	somatomotor	dorsal attn	default*	default	control
	dorsal attn	visual	control	control	salience

*Note.* *most informative distribution, **largest but most uncertain effect
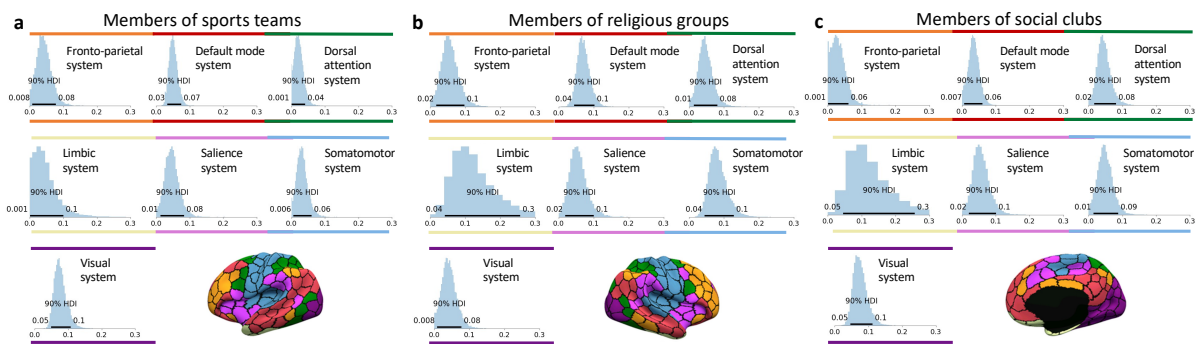
Figure 1. Three forms of social participation show strong network-wide effects in the default mode system and limbic systems. A Bayesian hierarchical framework was used to jointly analyze overall volume variation in seven major brain networks at the population-level (UK Biobank cohort with n = ~ 40.000 participants), separately to identify members of sports teams (**a**), religious groups (**b**) and social clubs (**c**). Contributions exhibit the amount of variance explained by every distributed canonical network, according to the 10-90% highest posterior density interval (HDI). A narrow (wide) posterior parameter distribution posterior density stands for a certain (uncertain) effect. A more positive (less positive) value for the mean posterior parameter density (x axis, sigma parameter) indicates for a higher (lower) explained variance across the dependent spatially distributed atlas regions in that network. By rough analogy to classical ANOVA, the network definitions could be viewed as "factors" and the region definitions could be viewed as "levels". Results are adjusted for effects of age and sex.
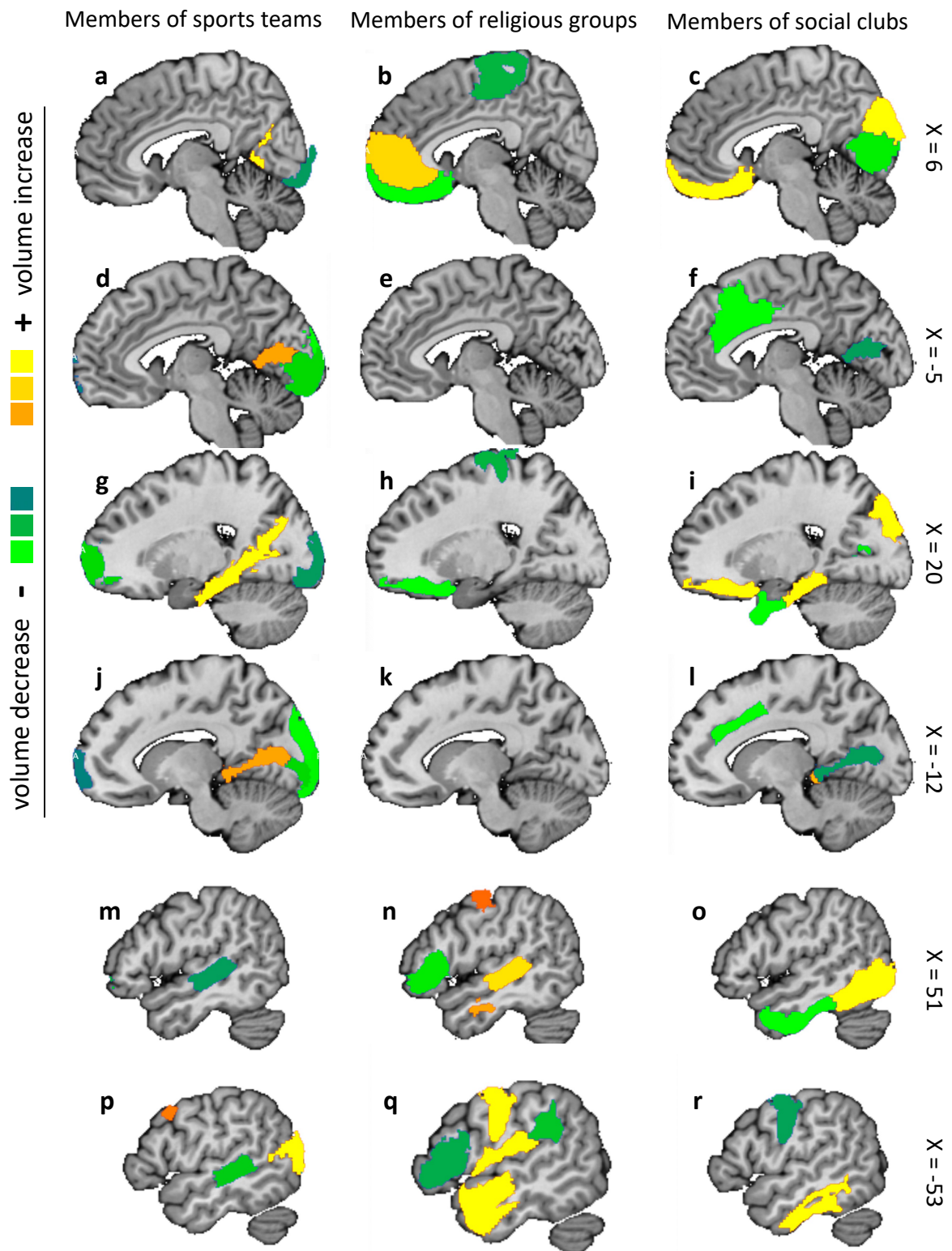
Figure 2. Population associations with regions of the default and limbic systems dominate the neural correlates of social participation. At the region level, our Bayesian hierarchical model identified for which brain regions variability in grey matter volume explains participants' reported weekly engagement in social groups. Strongest associations to day-to-day social support (cf. Fig. 1) were determined based on effect sizes (mean parameter) of the marginal posterior parameter distributions (volume measures in standard units). In the context of our modeling solution, the ventromedial

1210 prefrontal cortex showed no volume deviation in right hemisphere of (**a**) sport teams
1211 participants. A ventromedial prefrontal gray matter decrease was shown in (**b**) religious
1212 groups (light green) and a substance increase in participants of (**c**) social clubs
1213 (yellow). The anterior cingulate cortex showed no volume deviation in (**d**) sports team
1214 members in members of (**e**) religious groups in the left hemisphere. A volume decrease
1215 in the anterior cingulate cortex was instead shown in members of (**f**) social clubs (light
1216 green). The parahippocampal area showed a volume increase within the group of (**g**)
1217 sports teams (yellow) and (**i**) social clubs (yellow), while no volume deviation was
1218 shown for (**h**) religious groups. For the lingual gyrus, positive and negative volume
1219 effects were shown for (**j**) sports teams, and no volume effects for (**k**) religious groups.
1220 Negative volume effects were shown for (**l**) social clubs. Within the temporal lobe of
1221 sports team members (**m, p**)**,** both hemispheres had negative volume effects in the
1222 superior and middle temporal gyrus (green). For members of religious groups (**n, q**)**,**
1223 volume decrease in both hemispheres was demonstrated in superior and middle
1224 temporal gyrus (yellow). The social club participants (**o, r**) showed a volume decrease
1225 (green) in right hemisphere and volume increase in left hemisphere in fusiform gyrus
1226 and inferior temporal gyrus.

1227
1228
1229
1230
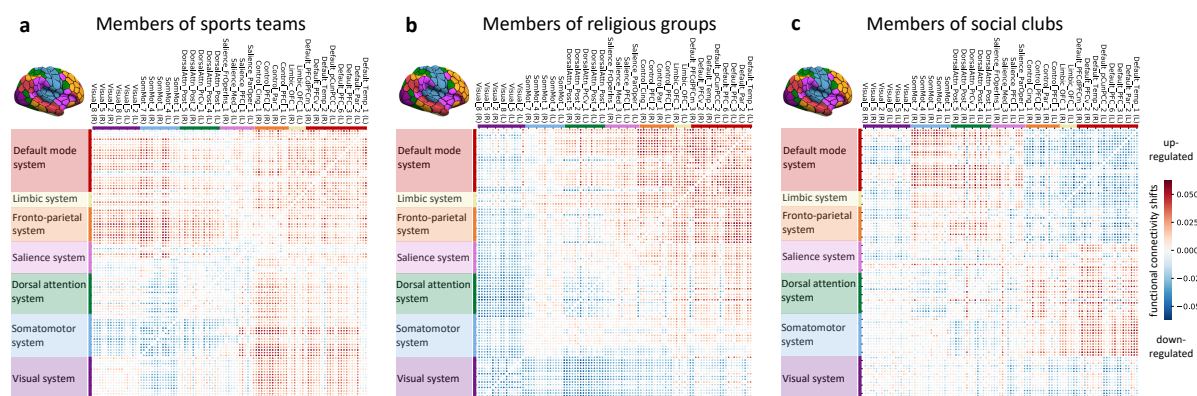
1231
1232
1233 **Figure 3. Signatures of functional coupling fluctuations highlight the relevance**
1234 **of intra- and inter-network deviations of the default and limbic network in social**
1235 **participation**. Functional connectivity shifts are shown for the dominant population
1236 mode related to weekly social participation (connectivity links in standard units). The
1237 leading mode identified positive (red) and negative (blue) shifts in network connectivity
1238 using a pattern-learning algorithm, with statistical significance at *p* < 0.05 (one-sided
1239 test) using nonparametric permutation testing. The intra- and inter-network connectivity
1240 is depicted for the participants of (**a**) sports teams, (**b**) religious groups and (**c**) social
1241 clubs. L/R refers to left and right hemisphere. The default and limbic network showed
1242 an increase in connectivity strengths in members of sport teams and religious groups
1243 and a decrease in members of social clubs.
1244
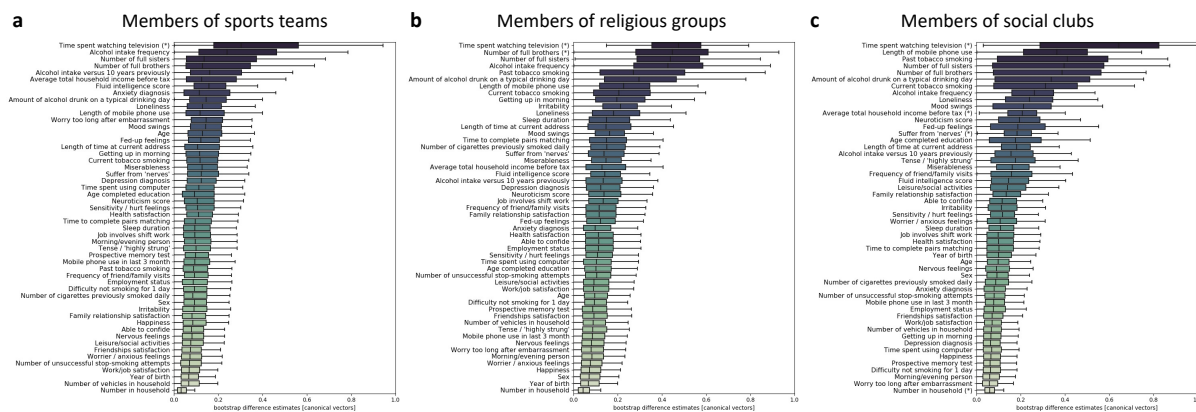
Figure 4. Demographic profiling analysis pinpoints indicators of mental health, smoking and alcohol consumption consistently across three groups of social participation. Multivariate pattern-learning (cf. Methods) was used to explore how the top brain regions (see Fig. 2) are linked to a variety of behavioral indicators with their robust cross-links to weekly social participation. Behavioral measures covered domains of mental and physical well-being, lifestyle choices, and social embeddedness. In 1,000 bootstrap resampling iterations, our entire pattern-learning pipeline in grey matter volume was repeated separately in the two participant groups: UK Biobank participants who regularly share life experience with close others and those with little such exchange of personal events. The computed differences in brain-behavior associations between both groups (i.e., dominant canonical vector entries) were gathered across the 1,000 perturbed realizations of our original dataset to obtain faithful bootstrap intervals. These estimates of uncertainty directly quantified how group-related deviations vary in the wider population. Asterisks indicate statistical relevance based on excluding zero between the 5/95% quantiles of the bootstrap distribution. These brain-behavior associations showed great correspondence for regular intake of alcohol and tobacco as well as multifaceted aspects of psychological well-being across participants of (**a**) sports teams, (**b**) religious groups and (**c**) social clubs. Further consistent findings across all three forms of social participants included the time spent watching television, number of siblings and further mental health conditions. The boxplot whiskers depict the interquartile range.