Population level interactions between the neural correlates of dispositional internal thought and visual imagery

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Abstract

Experience is not always tied to events taking place in the environment. We often generate thoughts, images and feelings unrelated to the events in the here and now. Important aspects of these self-generated experiences are stable over time within an individual but are also associated with various dispositional traits (such as ADHD or depression). In our current study, we explored whether task-free functional imaging can shed light on whether these associated dispositional features depend on common or distinct underlying mechanisms. We acquired resting state functional magnetic resonance imaging data from a large cohort of participants and sampled their experience during the scan by asking them to retrospectively report their thoughts. In a separate experimental session, participants completed a battery of measures reflecting a range of different dispositional traits. Independent component analysis identified a set of whole-brain functional networks, and we modelled how the associations between each of these nodes correlated with metrics of ongoing thought at rest as well as with dispositional indices of physical and mental health. Behaviourally, we found evidence of association between patterns of ongoing experience emphasising visual imagery and aspects of disposition that reflected high levels of self-consciousness, depression and attentional problems. We found that increased connectivity between a posterior parietal network and a lateral fronto-temporal network was associated with more reports of visual imagery at rest. Furthermore, a pattern of decoupling between the brainstem and a lateral visual network was associated with dispositional internal focus (elevated self-consciousness, rumination and attentional problems). Critically, we found that these two brain-cognition relationships were related: the correlation between parietal-frontal regions and reports of visual imagery was stronger for individuals who also had stronger connectivity between aspects of the brain stem and cerebellum with visual cortex. Together, these results suggest that unique patterns of neural organisation reflect trait variance both in ongoing patterns of thought at rest and associated dispositional traits. Furthermore, our results suggest that accounting for trait-like dispositional patterns associated with different patterns of ongoing experience is important when exploring the neural mechanisms supporting different elements of self-generated experience.

Introduction

Whether we are thinking about a task at hand or mind-wandering about our future plans, our restless brain (Raichle, 2011) drives our restless mind (Smallwood and Schooler, 2006) at any given point in time. Investigating this dynamic relationship, recent studies have identified thematic patterns, or "dimensions" of thought, (Wang et al., 2018b) that have a reproducible structure across studies and time (Medea et al., 2018; Smallwood et al., 2016; Poerio et al., 2017; Konishi et al., 2017; Sormaz et al.,

2018). Recurring themes in experience capture variation in the content and form of our thoughts (Gorgolewski et al., 2014) and highlight stable patterns, such as thoughts about the future or the past (Ruby et al., 2013; Smallwood et al., 2016; Karapanagiotidis et al., 2017), the modality within which experience unfolds, i.e. whether it is dominated by imagery or inner speech (Wang et al., 2018a; Konishi et al., 2017; Smallwood et al., 2016), or the level of subjective detail (Sormaz et al., 2018; Smallwood et al., 2016; Gorgolewski et al., 2014).

These patterns of thought have associations with dispositional variables related to affect, psychological well-being, and problems in attention. For example, the temporal focus of spontaneous thoughts is linked to levels of happiness. Future thinking has been shown to improve mood (Ruby et al., 2013; Engert et al., 2014) and facilitate problem solving by refining future goals (Baird et al., 2011; Medea et al., 2018; McMillan et al., 2013). By contrast, thinking about the past is associated with negative mood (Ruby et al., 2013; Killingsworth and Gilbert, 2010) and in the case of intrusive, ruminative thoughts, to depression and anxiety (Watkins, 2008). In addition, identified patterns of spontaneous thought have been linked to creativity and intelligence (Baird et al., 2012; Wang et al., 2018b; Turnbull et al., 2019b) as well as ADHD (Seli et al., 2015), neuroticism (Perkins et al., 2015) and measures of self-consciousness (Smallwood et al., 2002). These studies demonstrate that different themes of ongoing thought are likely to be partly influenced by population variation in a range of dispositional variables.

These associations between specific dispositional variables and patterns of ongoing experience highlight a methodological challenge for the increasing number of studies that explore their neural correlates. For example, a popular line of investigation examines the hypothesis that the default mode network (DMN, Raichle et al., 2001) plays a particularly important role in self-generated thought (i.e. Andrews-Hanna et al., 2014). Consistent with this view studies, which combine experience sampling with online neural measures, have shown that core regions of the DMN, such as the posterior cingulate cortex (PCC) and the medial prefrontal cortex (mPFC), can have greater activity when patterns of ongoing thought shift from task relevant information (Mason et al., 2007; Christoff et al., 2009; Allen et al., 2013; Stawarczyk et al., 2011, although see Sormaz et al., 2018). Studies suggest the PCC may be an integrative hub associated with the content and form of thoughts (Smallwood et al., 2016), while connectivity between the hippocampus and the mPFC has been linked to episodic contributions to ongoing experience (Karapanagiotidis et al., 2017). Likewise, increased low frequency fluctuations in the PCC have been associated with greater imagery (Gorgolewski et al., 2014). However, studies have also shown that the patterns of default mode network connectivity are also predictive of mindfulness (Mooneyham et al., 2016), attention deficit disorder (Castellanos et al., 2008), depression (Sheline et al., 2009), and life satisfaction and unhappiness (Smith et al., 2015; Luo et al., 2015), each of which have associations with patterns of ongoing thought (Mindfulness, Mrazek et al., 2012b; ADHD, Seli et al., 2015; Vatansever et al., 2018; Depression and unhappiness, Smallwood and O'Connor, 2011). Together, such evidence indicates that while regions within the DMN play a role in patterns of ongoing experience, they are also implicated in dispositional traits that are associated with aspects of the experience within the general population.

More recent studies have highlighted neural processes outside the DMN that make an important contribution to ongoing cognition, either directly or by supporting dispositional traits that are linked to patterns of experience. Executive (Christoff et al., 2009; Mooneyham et al., 2017; Golchert et al., 2017; Godwin et al., 2017) and attention systems (Wang et al., 2018a; Chou et al., 2017; Turnbull et al., 2019a) have been related to variations in spontaneous thoughts. At the same time, neural patterns within the fronto-parietal system have been linked to intelligence (Finn et al., 2015), a

dispositional trait that has links with ongoing experience (Turnbull et al., 2019b; Mrazek et al., 2012a). Likewise, resting state functional connectivity of networks associated with social, affective, mnemonic and executive systems has been linked to different personality traits (Nostro et al., 2018), which have been shown to relate to different patterns of ongoing thought (Kane et al., 2017; Robison et al., 2017; Smeekens and Kane, 2016). Alterations in the stable functional interactions of large-scale networks at rest have also been observed in studies of psychological disorders, like ADHD (Fair et al., 2013; Hoekzema et al., 2014), generalised anxiety (Rabany et al., 2017), obsessive compulsive disorder (Jung et al., 2013; de Vries et al., 2017) and major depression (Greicius et al., 2007, Wang et al., 2012 for a review), all linked with variations in spontaneous thought (ADHD, Seli et al., 2015; Vatansever et al., 2018; OCD, Seli et al., 2017; Anxiety and depression, Nolen-Hoeksema, 2000; Watkins, 2008).

Current study

It is clear, therefore, that (i) patterns of ongoing thought show a complex relationship to other dispositional traits at a population level and (ii) both of these psychological dimensions share similarities at the neural level. In this study, we set out to understand the relationship between trait variance in patterns of ongoing thoughts, dispositional features and neural organisation. We acquired retrospective descriptions of ongoing thoughts while participants underwent a resting state functional magnetic resonance scan (rs-fMRI). In a separate session, we acquired measures of dispositional traits spanning both physical and mental health. We then calculated the functional connectivity of whole-brain functional networks and investigated how these functional interactions relate to ongoing cognition and psychological traits, as well as whether there are any neural patterns that can shed light on their shared features. We hoped that these analyses would highlight the interactions between multiple large-scale networks as important for both patterns of ongoing thought, and for psychological traits.

Methods

Participants

206 healthy participants were recruited by advert from the University of York. Written consent was obtained for all participants and the study was approved by the York Neuroimaging Centre Ethics Committee. 37 participants were excluded from analyses due to technical issues during the neuroimaging data acquisition, excessive movement during the fMRI scan (mean framewise displacement > 0.3 mm and/or more than 15% of their data affected by motion) (Power et al., 2014) or not completing the whole battery of behavioural tasks, resulting in a final cohort of N = 169 (111 females, $\mu_{age} =$ 20.1 years, $\sigma_{age} = 2.3$).

Behavioural methods

We sampled the participants' experiences during the resting state fMRI scan by asking them at the end of the scan to retrospectively report their thoughts, using a series of self-report questions. These items were measured using a 4-scale Likert scale with the question order being randomised (all 25 questions are shown in SI Table 1). In order to assess the participants' physical and mental health, we administered well-established surveys at a later separate session outside of the scanner. Details about each questionnaire are presented in SI. Analyses controlled for age, gender and motion during the resting state fMRI scan.

Neuroimaging methods

MRI data acquisition

MRI data were acquired on a GE 3 Tesla Signa Excite HDxMRI scanner, equipped with an eight-channel phased array head coil at York Neuroimaging Centre, University of York. For each participant, we acquired a sagittal isotropic 3D fast spoiled gradient-recalled echo T1-weighted structural scan (TR = 7.8 ms, TE = minimum full, flip angle = 20°, matrix = 256x256, voxel size = 1.13x1.13x1 mm^3, FOV = 289x289 mm^2). Resting-state functional MRI data based on blood oxygen level-dependent contrast images with fat saturation were acquired using a gradient single-shot echo-planar imaging sequence with the following parameters: TE = minimum full (≈19 ms), flip angle = 90°, matrix = 64x64, FOV = 192x192 mm^2, voxel size = 3x3x3 mm^3 TR = 3000 ms, 60 axial slices with no gap and slice thickness of 3 mm. Scan duration was 9 minutes which allowed us to collect 180 whole-brain volumes per participant.

fMRI data pre-processing

Functional MRI data pre-processing was performed using the Configurable Pipeline for the Analysis of Connectomes (C-PAC) (Craddock et al., 2013). Pre-processing steps included motion correction by volume realignment (Friston 24-Parameter Model) (Friston et al., 1996), nuisance signal regression of the 24 motion parameters calculated in the previous step plus five nuisance signals obtained by running a principal component analysis on white matter and cerebrospinal fluid signals using the CompCor approach (Behzadi et al., 2007), slice time correction, temporal filtering 0.009-0.1 Hz, spatial smoothing using a 6mm Full Width at Half Maximum of the Gaussian kernel and normalisation to MNI152 stereotactic space (2 mm isotropic) using linear and non-linear registration (boundary-based registration) (Greve and Fischl, 2009). No global signal regression was performed.

Group-ICA spatial maps

In order to reduce the dimensionality of the resting state fMRI data, following pre-processing, the data were masked by a 20% probabilistic whole-brain grey matter mask, temporally demeaned, had variance normalisation applied (Beckmann and Smith, 2004) and were fed into the MIGP algorithm (Smith et al., 2014). The output of MIGP, which is a very close approximation to running PCA on the temporally concatenated data, was then fed into group-ICA using FSL's MELODIC tool (Beckmann and Smith, 2004), where spatial-ICA was applied, resulting in 16 distinct group-ICA spatial maps. We chose this number of components in order to identify large-scale functional networks resembling those presented in previous studies that deployed similar dimensionality reduction algorithms (i.e. Yeo et al. 2011). On visual inspection of the derived components, one was marked as artefactual and removed. These group spatial maps were subsequently mapped onto each subject's pre-processed data by running the first stage in a dual-regression analysis, which produced one time series per map per participant. The 15 spatial maps were named based on the top-loading term acquired from decoding each map on Neurosynth (Yarkoni et al., 2011) and are shown in Figure 1. This naming convention was extremely accurate for most maps, however, there were a few cases where the spatial ICA maps were slightly more extensive compared to the ones they were named after based on the Neurosynth decoding (i.e. the "language" and the "precuneus" maps). In Figure 1, we present the more generic names for these cases in brackets along with the Neurosynth generated ones.

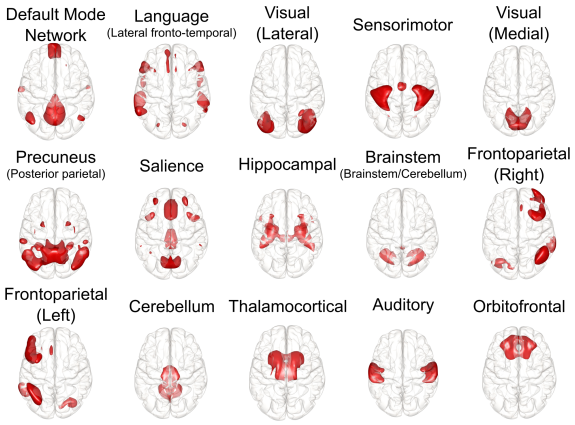

Figure 1. *ICA decomposition of fMRI data.*The panel shows the 15 spatial maps obtained from an independent component analysis on the temporally concatenated fMRI data. The maps correspond to well-known whole-brain functional networks and were named based on the top-loading term acquired from decoding each map on Neurosynth.

Static functional connectivity

Network modelling was carried out by using the FSLNets toolbox. We calculated the partial temporal correlation between the 15 ICA components' timeseries, creating a 15 x 15 matrix of connectivity estimates for each participant. To improve the stability of the estimates of partial correlation coefficients, a small amount of L2 regularisation was applied (Smith et al., 2013a). The connectivity values were converted from Pearson correlation scores into z-statistics with Fisher's transformation (including an empirical correction for temporal autocorrelation). For group-level between-subject comparisons, we combined all participants' network matrices into one and ran a univariate general linear model combined with permutation testing (FSL's randomise (Nichols and Holmes, 2002), 5000 permutations) for each edge. Edge weight was the dependent variable and behavioural measures (thought questions or component loadings from the general and mental health PCA decomposition) the independent ones. We used FWE-correction to account for multiple comparisons and all analyses controlled for age, gender and motion (mean frame-wise displacement) during the rs-fMRI scan.

Results

Analytic aims

The aim of our study was to understand the complex relationship between patterns of ongoing thoughts, dispositional traits and their associated neural correlates. Accordingly, our analytic approach had three steps. First, we examined the pattern of association between disposition traits and stable features of ongoing experience. Second, we examined the neural correlates of both these psychological features. Third, we examined whether associations between patterns of ongoing experience and dispositional features observed within our population are also reflected in the combination of neural correlates we identified in the second step of our analysis.

Describing experience and well-being

In order to identify the measures of experience with the best reliability and thus the most trait-like features, we repeated the resting state scanning session for a subset of our sample (N = 40) approximately 6 months later. This revealed 6 questions the responses to which were consistent within individuals across sessions (Fig. 2a): normal thoughts (i.e. experiences that I often have, intraclass correlation coefficient = 0.28, p = 0.035), deliberate vs spontaneous thoughts (ICC = 0.27, p = 0.044), intrusive thoughts

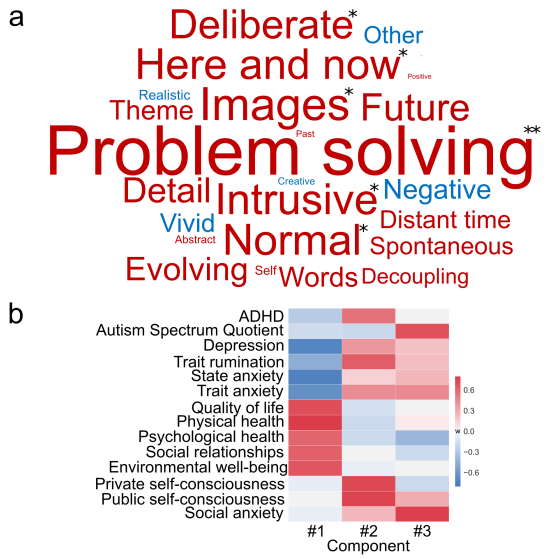

Figure 2. *Behavioural variables.* **a**) Test-retest reliability of responses to items at the end of two resting state fMRI scans for 40 participants. Intraclass correlation coefficient (ICC) visualised using a word cloud. Font size represents the absolute ICC value and font colour its sign (red for positive and blue for negative values). * $p < 0.05$, ** $p = 0.001$. **b**) Component weights from a principal component analysis on the participants' responses to dispositional measures of physical and mental health. Analyses controlled for age, gender and motion during the resting state fMRI scan.

(ICC = 0.29, p = 0.034), thoughts that took the form of attempts at problem-solving (ICC = 0.454, p = 0.001), thoughts about the here and now (ICC = 0.281, p = 0.036) and thoughts in the form of images (ICC = 0.3, p = 0.026). We used these items in subsequent analyses.

To reduce the dimensional structure of the measures of physical and mental health, we performed a principal component analysis (PCA) decomposition with varimax rotation. This identified three principal components with eigenvalues greater than 1 (Fig. 2b). Component 1 loaded positively on measures of quality of life and psychological well-being and negatively on indices of depression and anxiety, a component which we will refer to as well-being. Component 2 loaded on self-consciousness, attention deficit hyperactivity disorder (ADHD) and rumination, a pattern we refer to as internally directed attention. Component 3 loaded on social anxiety and autism and we refer to this pattern as reflecting social difficulties.

Comparing common variance in disposition and descriptions of ongoing experience at rest

Our first analytic goal was to explore the links between measures of well-being and self-reports of experience at rest within our sample. Using bivariate correlations, we found a positive correlation between well-being with 'normal' patterns of thoughts ($r = 0.17$, $p < 0.05$). Internally directed attention was associated with both patterns of intrusive thoughts ($r = 0.19$, $p < 0.05$) and of thinking in images ($r = 0.16$, $p < 0.05$). Finally, social difficulties were negatively associated with thinking in images ($r = -0.16$, $p < 0.05$). These analyses are presented in the form of a heat map in Figure 3a. To evaluate the multivariate associations between this set of variables, we ran a canonical correlation analysis (CCA) using the PCA components of the physical and mental health scores and the six reliable self-report items. This analysis yielded three canonical components, or modes, out of which the first was statistically significant using the Wilks's $\lambda = 0.823$ criterion, $F(18, 453.03) = 1.795$, $p = 0.023$, explaining 11.5% of the variance shared between the variable sets (modes 2 and 3 explained 4.1% and 3% of the remaining variance in the variable sets respectively). The variables' associations for the first CCA mode are shown in Figure 3b. Descriptions of experience as in the forms of images was the strongest experiential predictor of this mode (standardised canonical

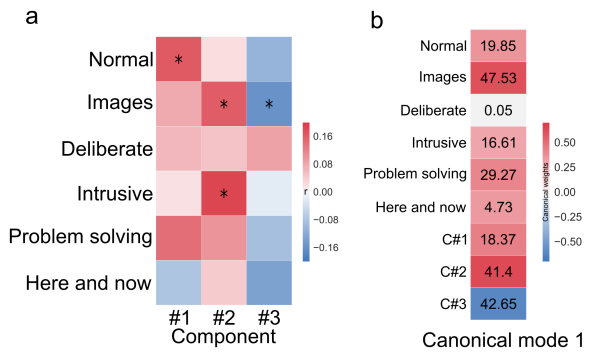

Figure 3. *Relationship between measures of well-being and self-reports of experience at rest.* **a**) Bivariate correlation between the 6 thought probes that were significantly reliable and the component scores from the PCA decomposition of physical and mental health scores. **b**) Heat map showing the standardised canonical weights of each item for the significant canonical mode 1. The annotations indicate the item variance explained by the CCA mode. Analyses controlled for age, gender and motion during the resting state fMRI scan.

weight = 0.62, r_s^2 = 47.53). It was also linked to patterns of internally directed attention (component 2, standardised canonical weight = 0.64, r_s^2 = 41.4) and to a relative absence of social difficulties (component 3, standardised canonical weight = -0.62, r_s^2 = 42.65).

Comparing common variance in patterns of neural organisation and descriptions of ongoing experience

Having identified the common variance shared by measures of disposition and reports of ongoing experience, our next analysis examined the relationship between static (time-averaged) functional connectivity of whole-brain networks and the experiential reports that individuals gave at the end of the scan. For each participant, we calculated the correlation between each whole-brain spatial ICA map (see Fig. 1), using partial instead of full correlation, as it is considered to be a good estimate of direct functional connections (Smith et al., 2013b). Figure 4 shows the average partial correlation matrix across subjects (thresholded for visualisation) in the form of a chord plot. Strong interactions highlight the relatively decreased correlation between the DMN and sensory networks, the auditory with the sensorimotor and the two visual networks forming synchronised pairs of sensory processing, and the precuneus with the salience networks as positively coupled.

We then explored the links between static functional connectivity and the six experiential reports with the most trait-like features. As we were interested in both focal and widespread effects, we chose to run our analyses using multiple edge weight thresholds that resulted in varying numbers of edges included in each analysis. Taking into account only the strongest edges on average across subjects (top 15% of partial correlation weights), we regressed the edges' partial correlations against participants' thoughts, while controlling for age, gender and motion during the rs-fMRI scan. Using permutation testing, we found that more positive correlations between the precuneus and the lateral fronto-temporal network for subjects reporting thinking more in images (Fig. 5a) (p = 0.016, FWE-corrected). The pattern remained significant for a lower correlation weight threshold that included weaker edges in the analysis (top 30% of partial correlation weights) (p = 0.037, FWE-corrected). No significant relationship was found for a threshold that kept the top 50% of connections and when no threshold was applied at all. This analysis highlights that an increase in a functional connection between the precuneus and the lateral fronto-temporal networks at rest was observed for people who rated their experience as taking the form of images.

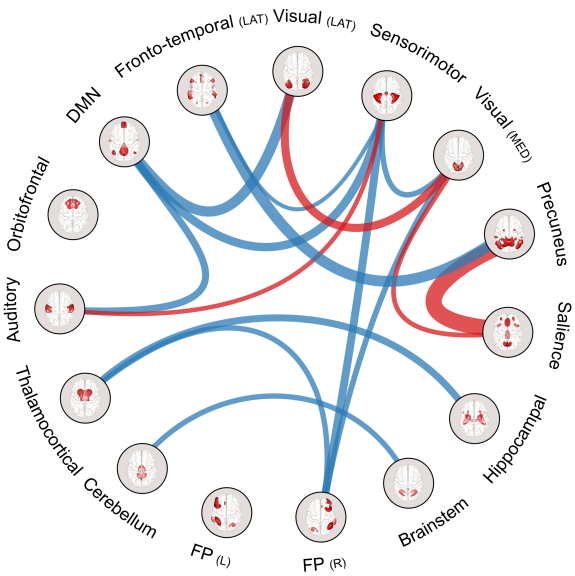

Figure 4. *Partial correlation of ICA maps.* Network circle graph of the average partial correlation matrix across subjects. The circle graph was thresholded at the 85th percentile of absolute z-values as estimated from an r to z Fisher's transformation. Red is for positive and blue for negative values and edge width is weighted by their absolute value. L:Left, R:Right, LAT:Lateral, MED:Medial.

Comparing common variance in patterns of neural organisation and dispositional traits

Using the same connection thresholds (top 15%, 30%, 50% and no threshold), we found that a lower correlation between the lateral visual and the brainstem networks was associated with increased internally directed attention (Fig. 5b). The link was significant for the top 50% of connections (p = 0.021, FWE-corrected) and when no threshold was applied (p = 0.05, FWE-corrected). That is, there was a decrease in the functional interaction between the brainstem and lateral visual networks for people who scored higher in dispositional internal focus.

Examining the relationship between neural "fingerprints" of disposition and patterns of ongoing experience

Together, our analyses suggest that reports of imagery at rest were associated with traits of internally directed attention (Fig. 3) and that both had reliable, yet distinct neural correlates. To understand if the identified neural patterns moderated the relationship between the psychological measures, we ran two multiple regression analyses; in one, the dependent variable was reports of visual imagery and in the other, dispositional internal focus (component 2, see Fig. 2). In each model, the remaining three scores were entered as predictors and we modelled their main effects and their three pairwise interactions (while controlling for age, gender, and motion during the resting state fMRI scan). The analysis with visual imagery as the dependant variable identified two main effects: thinking in images was positively correlated with the connectivity between the lateral fronto-temporal and precuneus networks (β = 0.19, p = 0.016) and with component 2 scores (β = 0.18, p = 0.026). Critically, it also indicated an interaction (β = 0.16, p = 0.043) suggesting that the correlations between the precuneus and lateral fronto-temporal regions and reports of imagery were stronger for participants who also had higher lateral visual and brainstem connectivity (associated with low loadings on internally focused attention). This is displayed in Figure 6 in the form of a scatter plot. The second analysis, with dispositional internal focus as the dependent variable identified two main effects, but not an interaction: internally focused attention was negatively correlated with the connectivity between the

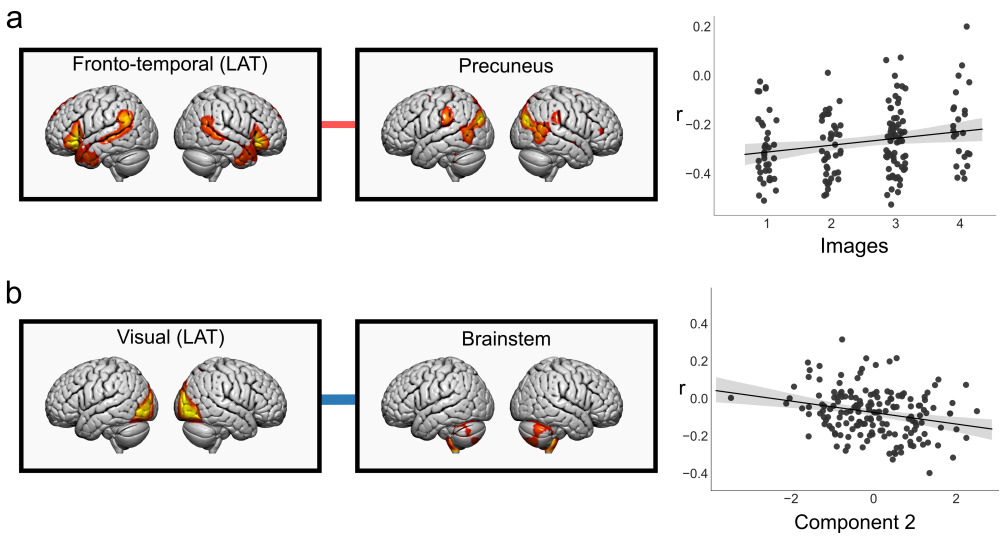

Figure 5. *Static functional connectivity associated with behaviour.* **a**) Left. The lateral fronto-temporal and precuneus networks. The edge highlights an increase in their partial correlation for people thinking more in images. Right. Scatter plot of thinking in images scores with correlation values between these two networks for each participant. **b**) Left. The lateral visual and brainstem networks. The edge highlights a decrease in their partial correlation for higher ADHD and rumination scores (PCA Component 2). Right. Scatter plot of Component 2 scores from the PCA of the physical and mental health questionnaires with correlation values between these two networks for each participant.

lateral visual and brainstem networks (β = -0.25, p = 0.001) and positively correlated with thinking in images (β = 0.17, p = 0.024).

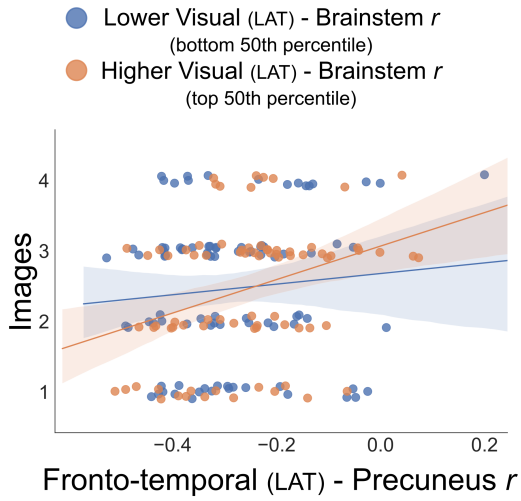

Figure 6. *Moderation effect of the lateral visual - brainstem coupling to the relationship between thinking in images and lateral fronto-temporal - precuneus functional connectivity.* The scatter plot shows the correlation values between the lateral fronto-temporal and precuneus networks and thinking in images scores grouped, by a median split, into higher and lower connectivity groups between the lateral visual and brainstem networks.

Discussion

This study set out to explore how associations between patterns of unconstrained ongoing experience and dispositional traits are reflected in the underlying neural architecture. Within our population we found a positive correlation between a style of thinking which emphasises visual imagery and a pattern of dispositional internal focus.

Both of these psychological features had distinct neural correlates. Thinking more in images was related to an increase in correlation between the precuneus and a lateral fronto-temporal network, while a decreased correlation between the lateral visual and a brainstem/cerebellar network was linked to internal attention. Critically, we found a significant interaction between these two neural traits: the correlation between precuneus - lateral fronto-temporal connectivity and visual imagery was more pronounced for individuals who also had stronger coupling between the brainstem/cerebellar network and visual cortex. Our results, therefore, indicate that there are distinct stable neural interactions that support ongoing experience as well as dispositional traits, and highlight there are indirect neural relationships that link these discrete phenomena together. In this discussion, we first consider the links between our findings and prior studies examining relationships between neural organisation and both ongoing thought and dispositional processes, before considering the implications of our findings for brain-experience correlations more generally.

Precuneus interactions with lateral frontal and temporal systems are important for visual imagery.

Prior studies have shown that thinking in the form of images is an important feature of ongoing experience (Andrews-Hanna et al., 2013; Delamillieure et al., 2010) and our study suggests that this process is linked to the functional organisation of the precuneus. Although posterior medial cortex is functionally heterogeneous (Margulies et al., 2009; Cavanna and Trimble, 2006), the precuneus has been related to visuospatial mental imagery (for a review see Fletcher et al., 1995), episodic memory retrieval of imagined pictures (Lundstrom et al., 2003) and imagining past episodes related to self (Lou et al., 2004). Our analysis suggests that visual imagery is linked to functional connectivity between the precuneus and regions of the temporal lobe that are thought to contribute to multi-modal forms of semantic cognition (Jefferies, 2013). Contemporary accounts, for example, suggest that the anterior temporal lobe supports cognition with different representational features (pictures versus words, Murphy et al., 2018; Vatansever et al., 2017; Ralph et al., 2017 for a review). Generally therefore, our results are consistent with the hypothesis that the production of visual imagery may depend upon the integration of a system important for visual processing (the precuneus), with regions that support multi-modal elements of cognition (lateral temporal and frontal cortex).

Lateral visual cortex and brainstem interactions relate to rumination, self-consciousness and ADHD

We also found that internally focused cognition was linked to reduced correlation between the brainstem/cerebellum and the lateral visual cortex. Previous studies have shown that brainstem abnormalities can support increased accuracy of diagnostic classification in ADHD (Johnston et al., 2014). Decreased axial diffusivity (a marker of axonal degeneration in clinical cases, Song et al. 2002) in the occipital lobe and brainstem has also been associated with an ADHD diagnosis (Gehricke et al., 2017). In addition, processes within the brainstem have been related to rumination, worry and anxiety by influencing heart rate variability (Porges, 2007; Aldao et al., 2013) and by its functional interactions with the limbic network in anxiety disorders (Engel et al., 2009). Our findings for increased rumination, self-consciousness and ADHD scores may highlight a functional neural configuration where visual input becomes increasingly incoherent with the activity of a network regulating autonomic functions and modulating global connectivity (Van den Heuvel and Sporns, 2013). This could indicate the reduced processing of sensory input that is thought to be important for periods of

internal focused experience (Smallwood and Schooler, 2015).

Interactions between neural correlates of disposition and patterns of ongoing thought

Importantly, our study not only identified patterns of neural organisation correlated with both visual imagery and internally focused attention, it also highlighted that the neural correlates of these associated traits interact in an important manner. Our results suggest that the association between precuneus-lateral fronto-temporal connectivity and reports of visual imagery was more pronounced for individuals who had stronger connectivity between regions of the brainstem and lateral occipital cortex. Based on our data, it is plausible that not only are patterns of visual experience linked to dispositional variance in internally focused attention, but their neural correlates interact in a complex way to produce the observed patterns of functional connectivity at rest. These observations suggest that studies exploring the cognitive significance of patterns of neural organisation, either in terms of understanding their relationships with disposition, or the nature of ongoing experience, would benefit by accounting for both types of traits in their analyses. Based on our study, understanding the dispositional influences on patterns of ongoing thought can help improve our understanding of the neural basis of ongoing experience. Likewise, our understanding of the neural mechanisms underlying patterns of dispositional traits which are associated with certain aspects of ongoing experience may be improved by accounting for features of the experience when neural activity is recorded. As well as the questionnaire administered in our study, there is now an emerging number of measures of ongoing experience such as the New York Cognition Questionnaire (Gorgolewski et al., 2014), the Amsterdam Resting State Questionnaire (Diaz et al., 2013) and Resting state questionnaire (Delamillieure et al., 2010). The low economic cost of these measurements and the ease of their administration suggest that collecting data on patterns of ongoing thought can improve our understanding of neural correlates of specific dispositional states. We recommend that in the future these sorts of measures become part of the standard resting state protocol.

Conclusion

In conclusion, our study highlights that neural functioning during rest relates to both ongoing experience and patterns of dispositional traits. Our test-retest analyses revealed recurring themes of spontaneous thoughts that remain relatively stable within individuals. These themes were associated with physical and mental health and ultimately linked to the static functional coupling between large-scale brain networks. Along with the unique neural functional patterns facilitating each behaviour, our results revealed an interaction between these relationships, demonstrating how neural and dispositional traits can influence ongoing cognition. Together, our findings complement previous studies investigating the neural structural (Karapanagiotidis et al., 2017; Bernhardt et al., 2014) and functional (Sormaz et al., 2018; Martinon et al., 2019) substrates of ongoing experience and suggest that its inherently dynamic nature is shaped by the stable functional interactions of the brain and can be better understood by accounting for trait behaviour.

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