Missing the forest because of the trees: slower alternations during binocular rivalry are associated with lower levels of visual detail during ongoing thought

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Abstract

Conscious awareness of the world fluctuates, either through variation in how vividly we perceive the environment, or when our attentional focus shifts away from information in the external environment towards information that we generate via imagination. Our study combined individual differences in experience sampling, psychophysical reports of perception and neuroimaging descriptions of structural connectivity to better understand these changes in conscious awareness. In particular, we examined (i) whether aspects of ongoing thought—indexed via multi-dimensional experience sampling during a sustained attention task—are associated with the white matter fibre organization of the cortex as reflected by their relative degree of anisotropic diffusion and (ii) whether these neurocognitive descriptions of ongoing experience are related to a more constrained measure of visual consciousness through analysis of bistable perception during binocular rivalry. Individuals with greater fractional anisotropy in right hemisphere white matter regions involving the inferior fronto-occipital fasciculus, the superior longitudinal fasciculus and the cortico-spinal tract, described their ongoing thoughts as lacking external details. Subsequent analysis indicated that the combination of low fractional anisotropy in these right hemisphere regions, with reports of thoughts with high levels of external details, was associated with the shortest periods of dominance during binocular rivalry. Since variation in binocular rivalry reflects differences between bottom-up and top-down influences on vision, our study suggests that reports of ongoing thoughts with vivid external details may occur when conscious precedence is given to bottom-up representation of perceptual information.

Keywords: ongoing thought; binocular rivalry; detail; diffusion tensor imaging; experience sampling; fractional anisotropy
show stronger coupling between the DMN and regions of visual cortex (Turnbull et al. 2019b), recruit the posterior cingulate more during periods of self-reference (Murphy et al. 2019) and show greater cortical thickness in the para-hippocampus (Ho et al. 2019). Although a link between the DMN and externally focused experience is surprising given the widely held assumption that the DMN was limited to internally focused, task unrelated experiences (e.g. Fox et al. 2005), this proposed link is nonetheless consistent with more recent findings. For example, studies indicate that people can perform tasks with high levels of efficiency when they are ‘in the zone’ (Esterman et al. 2013; Kucyi et al. 2016) or ‘on autopilot’ (Vatansever et al. 2017a). Thus, understanding the neural mechanisms underlying different patterns of experience is not only important for contemporary accounts of ongoing conscious thought (Smallwood and Schooler 2015) but may also be important for appropriately characterizing the function of different large-scale neural networks.

The current study aimed to elucidate the role that top-down visual processes play in different types of dissociation between ongoing experiences and environmental events. Traditionally, research into conscious experiences has emphasized that it is possible to understand the relationship between subjective awareness and the immediate sensory context using situations of bistable perception (such as the Necker Cube, or the phenomenon of binocular rivalry) because, in such contexts, awareness can change without a concomitant change in sensory input (Crick 1996). Situations of bistable perception provide relatively unambiguous indices of the top-down influence on vision because they discard low-level processes that contribute to the process of perception (e.g. sensory transduction). In this context, the dominance of one image during bistable perception is assumed to reflect the influence of top-down processes on vision. Consistent with the assumption that bistable perception depends on the balance between top-down and bottom-up influences on vision, neuroimaging studies suggest that rivalry depends on both processes taking place in visual regions (Tong et al. 2006) as well as higher-order brain regions (Knapen et al. 2011; Baker et al. 2015). Importantly, both default mode and attention systems are important in binocular rivalry: whereas disruptions to regions of the DMN, such as the posterior parietal lobe, tend to lengthen perceptual alternations during bistable perception (Carmel et al. 2010; Kanai et al. 2011), disruptions to nearby regions of parietal cortex, within the dorsal attention network, shorten perceptual alternations (Kanai et al. 2011).

Our study sought to extend our understanding of naturally occurring changes in ongoing experience by linking them to both changes in the structural organization of the cortex and to indices of the top-down influence on vision as estimated from binocular rivalry alternations. Specifically, we analysed data from a large cohort of individuals who had extensively described the contents of their ongoing experience during a laboratory task (for prior publications, see Sormaz et al. 2018; Wang et al. 2018; Ho et al. 2019; Turnbull et al. 2019a,b) and for whom we also acquired measures of binocular rivalry using a paradigm similar to that used in our prior study (see Baker et al. 2015). These individuals also had measures of structural connectivity provided by diffusion tensor imaging (DTI), which has highlighted neural processes linked to both binocular rivalry (Genç et al. 2011) and to patterns of ongoing thought in a prior study (Karapanagiotidis et al. 2017). In the study by Karapanagiotidis et al., we found a right-lateralized region of
white matter that had greater fractional anisotropy (FA) for individuals who tended to neglect the external environment to imagine events in the past or future instead of those in the here and now. The current study aimed to replicate the association between ongoing experience and the white matter architecture of the right hemisphere in a new set of participants, and explore whether this association was related to the relative balance between top-down and bottom-up influences on vision during binocular rivalry, as indexed by an individual’s reported experience during binocular rivalry.

The left hand panel in Fig. 1 describes the paradigm we used to measure ongoing experience during a sustained attention task (top left), and in which we measured their conscious experiences through the estimation of binocular rivalry during bistable perception (bottom left). Application of Principle Component Analysis (PCA) to the Multi-Dimensional Experience Sampling (MDES) revealed four components, which are displayed in the form of word clouds on the right hand side panel. The colour and size of the words indicate the loadings of each question (font size = strength of relationship and colour = direction: warm is positive, cool is negative). The labels we used to describe these components in the paper are presented in quotations.

Materials and Methods

Participants

One hundred and fifty healthy, right-handed, native English speakers, with normal or corrected-to-normal vision and no history of psychiatric or neurological illness (mean age = 20.19 and 92 were females) participated in the study. All participants had provided their written informed consent approved by the Department of Psychology and York Neuroimaging Centre (YNIC), University of York ethics committees, and were debriefed after completion of the study. Participants were either paid or given course credits for their participation.

Procedures

Participants arrived at YNIC where we acquired brain images including T1-weighted magnetic resonance imaging (MRI), resting state MRI and DTI. On subsequent days, participants took part in a comprehensive set of behavioural assessments that captured different aspects of cognition, including both the experience sampling task and other experimental tasks (including binocular rivalry). These tasks were completed over three sessions on different days, with the order of sessions counterbalanced across participants. The task in which ongoing experience was measured always took place at the beginning of these laboratory sessions.

Experience sampling

We measured patterns of ongoing cognition in a paradigm that manipulated memory load by using alternating blocks of 0-back (low-load) and 1-back (high-load) conditions (see top left panel of Fig. 1), with the initial block counterbalanced across individuals (see Turnbull et al. 2019b for a complete description of this task). Multi-dimensional Experience Sampling (MDES) was used to measure the contents of ongoing thought. On each occasion, participants reported their thoughts by responding to one of the 13 questions presented in Supplementary Table S1. Participants always rated their task focus first, and then described their thoughts at the moment before the probe on a further 12 dimensions. Participants always answered all questions and were probed on an average of 27 occasions during the task over
the three sessions of the experiment. The rationale behind our approach is that different patterns of thought can be identified as regularities in covariation with how the questions are answered. These patterns can be quantified by applying statistical techniques, such as principal components analysis (PCA), to the experience sampling data. In this context, the dimensions produced by the application of PCA to MDES data acted as proxies for different thought patterns. Prior studies have shown that the patterns identified in this manner are robust to different samples of participants (Smallwood et al. 2016), consistent across situations (e.g. during scanning and in the behavioural laboratory, Sormaz et al. 2018) and show a degree of correspondence between experiences in the real world and in the laboratory (Ho et al. 2020).

Binocular rivalry

We showed rivalling stimuli to participants for four trials of 120 s in duration and asked them to report their perceptions using a computer mouse. The stimulus consisted of oblique gratings (1c/deg; 50% contrast, ±45 deg, 6 deg in diameter, smoothed by a raised cosine envelope) shown to opposite eyes (see bottom left panel of Fig. 1). All stimuli were presented on a gamma-corrected Iiyama VisionMaster Pro 510 cathode-ray tube (CRT) monitor with a mean luminance of 32 cd/m² and were viewed through a mirror stereoscope to permit presentation of different images to the left and right eyes. The stimuli were surrounded by a dark ring and a binocular Voronoi texture to promote binocular vergence and fusion (Baker and Graf 2009). Participants held down one mouse button when they perceived a particular percept (e.g. a left-oblique grating) and the other when they perceived the alternative (e.g. a right-oblique grating). If they simultaneously perceived both percepts, or experienced a mixed percept, they held down both buttons. This allows our paradigm to reveal the duration of time in which one percept dominated the other, as well as situations when both images were perceived at the same time. We counterbalanced the orientations of the rivalling stimuli between the eyes on alternate trials.

Diffusion tensor imaging

The DTI scan lasted 13 min. A single-shot pulsed gradient spin-echo echo-planar imaging (EPI) sequence was used with the following parameters: b = 1000 s/mm², 45 directions, 7 T2-weighted EPI baseline scans, 59 slices, FOV = 192 × 192 mm², TR = 15 s, TE = 86 ms (minimum full), voxel size = 2 × 2 × 2 mm³, matrix = 96 × 96. DTI data preprocessing steps involved eddy-current distortion correction and motion correction using FMRIB’s Diffusion Toolbox (FDT) v3.0, part of FMRIB Software Library (FSL) (Smith et al. 2004). FA was calculated by fitting a tensor model at each voxel of the preprocessed DTI data and the resulting images were brain-extracted using Brain Extraction Tool (BET) (Smith 2002). Voxelwise FA maps were analysed using tract-based spatial statistics (TBSS) (Smith et al. 2006). After participants’ FA data were non-linearly aligned to FMRIB58_FA standard space, they were transformed to the mean space of these subjects and then affine transformed to the 1-mm MNI152 space. Next, the mean of all FA image was created and thinned to create a mean FA skeleton representing the centres of all tracts common to the group.

The skeletonized FA images were then fed into voxelwise statistics, using FSL’s randomize command (a non-parametric permutation inference tool). Using a generalized linear model (GLM), the measured FA values across the skeleton were regressed with the experience sampling results, while age and gender were included as nuisance covariates. T-statistic maps for contrasts of interest were calculated with 5000 permutations (Nichols and Holmes 2002). Resulting maps were thresholded at a family-wise error (FWE) corrected P-value of 0.05 using threshold-free cluster enhancement (TFCE) (Smith and Nichols 2009).

Probabilistic diffusion models were also fitted using Bayesian Estimation of Diffusion Parameters Obtained using Sampling Techniques (BEDPOSTX) (Behrens et al. 2003), with 2 fibres modelled per voxel for 1000 iterations. Probabilistic tractography was performed using probabilistic tracking with crossing fibres (ProbTrackX) (Behrens et al. 2007) to reconstruct fibres passing through the region of interest (ROI) resulted from the above GLM analysis if high degree of cross fibres existed (see Associations with white matter fibre organization section). Tractography was performed in native diffusion space by transforming the ROI as seed masks from standard space into diffusion space using the inverse of the non-linear registration calculated in the TBSS pipeline. We used standard parameters (5000 samples/voxel, curvature threshold 0.2, step length 0.5 mm, samples terminated after 2000 steps or when they reached the surface as defined by a 40% probabilistic whole-brain white-matter mask). Connectivity maps of each individual were thresholded at 1% of total samples, mapped to standard space using non-linear registration and concatenated into a single 4D file.

Results

Categorizing experience

Binocular rivalry

Two metrics were calculated using data from the bistable perception session. The first was the mean duration (in seconds) of each period where one stimulus continuously dominated experience (dominance duration). Mean dominance duration shows robust and stable individual differences (Pettigrew and Miller 1998), which have previously been shown to be associated with connectivity between regions of parietal cortex (Baker et al. 2015), as well as the concentration of inhibitory neurotransmitters (gamma-aminobutyric acid, GABA) in visual regions of the brain (van Loon et al. 2013). Dominance durations are also affected by various personality types (Antinori et al. 2017a,b) and clinical conditions including autism (Robertson et al. 2013), bipolar disorder (Pettigrew and Miller 1998; Miller et al. 2003) and schizophrenia (Xiao et al. 2018; Ye et al. 2019). The second metric was the time when neither percept dominated experience, and so corresponds to the amount of time that participants reported seeing both percepts (mixed). Mixed percepts occur at transitions between states of full dominance, and involve a network of frontal and parietal brain areas, particularly in the right hemisphere (Knappen et al. 2011). Measures of these metrics were then transformed into z-scores, with outliers (~2.5, and based on visualization of boxplot generated in SPSS 25) being replaced with mean values (number of outliers: ‘dominance duration’ = 23, ‘mixed’ = 11). We found no correlations on the scores of these two metrics (r = 0.02, P < 0.9).

Experience sampling

In our analysis, we used the decomposition reported by Sormaz et al. (2018, see original paper for complete details). In brief, PCA was applied to MDES data at the trial level as standardized in our other works (e.g. see Smallwood et al. 2016; Konishi et al.
This produced four components: (i) ‘Detail’, reflecting patterns of detailed visual task-related experience, (ii) ‘Off-task thought’, dissociating on-task thoughts from episodic self-relevant thoughts, (iii) ‘Modality’, distinguishing thoughts related to images or words and (iv) ‘Emotion’ describing the affective tone of experiences. These components are presented in the form of word clouds in the right hand panel of Fig. 1.

**Associations with white matter fibre organization**

Our first analysis examined associations between white matter connectivity and patterns of ongoing thought identified using MDES data. We conducted a multiple regression in which individual participant’s skeleton wide FA map was the dependent variable. Individual’s scores for each of the experiential dimensions identified through PCA were explanatory variables. Age and gender were included as nuisance covariates. Significant negative associations between FA and detailed thoughts were identified, and regions showing this relationship are presented in red in Fig. 2.

Next, we examined the relationship between the current result and those from our prior study (Karapanagiotidis et al. 2017). In Karapanagiotidis et al. (which used a different set of participants), we identified a set of right-lateralized tracts with greater FA for individuals reporting more mental time travel. Comparison of the two FWE-corrected maps indicated an area of overlap (see bottom right panel in Fig. 2). Karapanagiotidis et al. found higher FA linked to experiences characterized by self-generated thoughts about the past and the future, while the current results highlighted lower FA was linked to more detailed assessments of the here and now. Together, these results provide converging evidence that right-lateralized white matter tracts are important for differences in internal versus external focus of attention. As this region of overlap has a high degree of crossing fibres, we used ProbTrackX to estimate the white matter bundles to which this was most likely to be related (see Materials and Methods section, bottom left panel of Fig. 2). It can be seen that the results of this process highlighted multiple large fibre bundles including the inferior occipital-frontal (IFOF) and the cortico-spinal tract (CST), and the superior longitudinal fasciculus (SLF).

**Associations between different features of conscious experience**

Having documented associations between white matter structures and ongoing thoughts, we next examined (i) whether patterns of ongoing experience identified by MDES are related to the nature of experience as determined via binocular rivalry, and, if so, (ii) whether these relationships are linked with the associated white matter architectural differences in brain

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**Table 1. Simple correlations between z-scored measures of ongoing experience (represented as the rows) and z-scored metrics of bistable perception (represented in the columns)**

<table>
<thead>
<tr>
<th></th>
<th>'Dominant'</th>
<th>'Mixed'</th>
</tr>
</thead>
<tbody>
<tr>
<td>Detail</td>
<td>r = -0.12</td>
<td>0.13</td>
</tr>
<tr>
<td></td>
<td>p = 0.13</td>
<td>0.13</td>
</tr>
<tr>
<td>Off-task</td>
<td>r = -0.07</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>p = 0.42</td>
<td>0.57</td>
</tr>
<tr>
<td>Modality</td>
<td>r = -0.07</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>p = 0.41</td>
<td>0.94</td>
</tr>
<tr>
<td>Emotion</td>
<td>r = -0.07</td>
<td>0.14</td>
</tr>
<tr>
<td></td>
<td>p = 0.42</td>
<td>0.09</td>
</tr>
</tbody>
</table>

r = Pearson correlation; p = P-value.
structure. Table 1 shows the zero-order relationships across this set of variables.

To formally understand the relationship between different patterns of thought, their observed associations with white matter architecture, and the estimates of experience provided by binocular rivalry, we conducted a multivariate analysis of covariance. In this analysis, mean dominance duration and the proportion of mixed percepts were the dependent variables. The explanatory variables were individual scores on each PCA dimension, as well as the DTI correlate of detailed experience (i.e. the mean FA for the white matter region that is correlated with 'Detail' experience). Age and gender were included as nuisance covariates. We modelled the main effect of each explanatory variable, as well as the interaction between 'Detail' and its white matter correlate. We found a significant interaction between 'Detail' and its association with white matter connectivity \([F(2, 140) = 4.8, P = 0.011\), partial eta squared \(= 0.06\)], reflecting differences in mean dominance duration \([F(1, 149) = 7.43, P = 0.007\), partial eta squared \(= 0.05\)]. To visualize this association, we plotted the relationship between FA separately for individuals with high and low 'Detail' experience (using median split). It can be seen that the shortest dominance durations were observed among individuals with high levels of 'Detail' and the lowest FA (see left hand panel of Fig. 3). Notably we did not find any association between off-task thought and binocular rivalry, nor with white matter architecture suggesting a relatively specific relationship with highly detailed externally focused experience.

**Discussion**

Our study set out to better understand the neural basis of different types of shift in the quality of conscious experience by leveraging on methods of experience sampling, binocular rivalry and structural brain imaging. We found a correlation between individual differences in estimates of the integrity of cortical white matter in the right hemisphere and the level of detail with which external events were experienced. Notably, the pattern of right-lateralized white matter tracts that had greater integrity for less detailed experiences in the current analyses overlapped with our prior analysis using a different sample. Our prior study highlighted greater FA for individuals with a greater focus away from the moment to other times and places (Karapanagiotidis et al. 2017). Given that external focus is reduced during periods of self-generated imaginative thought (Kam et al. 2011; Kam and Handy 2013), these two results help establish the importance of a right-lateralized network of white matter tracts in determining aspects of cognition as assessed by experience sampling.

We found an interaction between the measure of detailed experience and its associated white matter correlate with patterns of dominance reported during bistable perception. In particular, individuals who reported higher levels of external details during sustained attention and had the lowest estimates of white matter integrity in these right-lateralized regions, also reported shorter periods when one percept dominated. It is usually assumed that, during binocular rivalry, top-down processes stabilize one potential interpretation of visual input, and so shorter time during rivalry is related to bottom-up influences on perception. Based on our data, our participants’ reports of detailed experience during sustained attention might emerge because of a conscious emphasis on bottom-up influences derived from sensory input that is, in turn, partly constrained by the white matter architecture of the cortex.

**Limitations and future directions**

Although our study suggests a relationship between detailed processing of external information, the white matter architecture of the cortex and patterns of dominance during rivalry, there are a number of important limitations that should be borne in mind when considering these results. First, based on our data, it seems possible that fluctuations in the degree of
task-relevant attention during binocular rivalry will impact upon the nature of how external information can dominate at a given moment in time. Our data cannot address this issue directly because we did not measure experience during the binocular rivalry session. It will be important in the future to measure the focus of individuals’ experience while they are exposed to rivalrous stimuli to address this possibility. Second, alternative measures of tractography are able to detect non-Gaussian features of FA (Cohen-Adad et al. 2008) and it may be worthwhile using these metrics in future studies examining associations with cognition and the white matter structure of the cortex. Third, it is possible that the measure of rivalry, which depends on the participants’ ability to recognize the switches in their conscious experience, may under-represent the actual number of shifts, particularly for participants who lack meta-awareness of their ongoing thought patterns (Schoolder 2002). In future studies, this limitation could be addressed by intermittently probing individuals to determine which percept they were currently consciously attending to.

We close by considering the possibility that the fibre bundles identified through probabilistic tractography in our study may offer a possible window into how the DMN can contribute to modes of operation that have both internal and external features. An emerging puzzle in cognitive neuroscience is the role that the DMN plays in cognition. Initial views of this system suggested that it was linked primarily to internal states of ongoing experience that were broadly unrelated to external task performance (e.g. Fox et al. 2005). However, evidence implicating this system in external tasks (Esterman et al. 2013; Smallwood et al. 2013; Konishi et al. 2015; Vatansever et al. 2015, 2017b; Murphy et al. 2018, 2019) coupled with our prior demonstrations of a role of the DMN in patterns of detailed thought (Smallwood et al. 2016; Sormaz et al. 2018; Turnbull et al. 2019a,b) challenge the views of this large-scale system as important for purely internal thoughts. Our study identified a white matter region linked to patterns of detailed external thought that was at the overlap of three major white matter fibre bundles. The CST, which originates in regions of sensory and motor cortex with most axons crossing at the anatomical midline between brainstem and spinal cord, is the principal motor pathway for voluntary behaviour and is important for the modulation of sensory information (Kolb and Whishaw 2009; Welniarz et al. 2017). The SLF is a major white matter pathway that connects the frontal, parietal, temporal and occipital lobes (Kawamura and Naito 2013; Konishi et al. 2015; Batanowska et al. 2016). It is impossible to determine precisely which of these tracts has the most important link with experience because of limitations of the ability of DTI to distinguish crossing fibres (Jbabdi et al. 2010); however, emerging evidence suggests that these three tracts may be reasonable candidates for future studies to explore. For example, recent works have suggested that the microstructural architecture of the SLF is predictive of patterns of unpleasant brooding in depression and functional connectivity of a prefrontal white matter network within the broader DMN (Pinser et al. 2019), as well as the perception and experience of emotions (Ho et al. 2016). Similarly, Bonnelle et al. (2012) found that traumatic brain injury to a white matter path identified by probabilistic analysis led to less efficient regulation of neural activity within the DMN by the saliency network. Notably, we recently demonstrated that the saliency network plays a critical role in the adaptive allocation of conscious attention to both internal and external foci, in part through its relationship to both the DMN and to systems important for external attention, namely the dorsal attention network (Turnbull et al. 2019a). In future, it would be useful to explore how the structural architecture of the brain constrains the functional activity in the cortex and, in particular, the DMN, across situations varying in their reliance on internal and external modes of cognition.

Conclusions
Prior studies have implicated the DMN in task-relevant material, in particular, in experiences with an emphasis on detailed representations of task-relevant information. The current study combined experience sampling, measures of white matter architecture and indices of binocular rivalry. We found that a detailed focus on task-relevant information during sustained attention was linked to the integrity of white matter pathways in the right hemisphere. This association was linked to shorter periods of dominance during binocular rivalry. Together these results suggest that detailed representations of external task-relevant information may be associated with conscious emphasis on bottom-up influences derived from sensory input, that is, possibly constrained by the white matter architecture of the right hemisphere. Our study highlights the possibility that although the DMN is traditionally assumed to be linked to internal states, it may also be associated with task-relevant information under situations when there are particularly strong representation of bottom-up sensory signals in transmodal cortex.

Supplementary data
Supplementary data is available at NCONSCJournal online.

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Data Availability
Data are available on request.

Conflict of interest statement. None declared.

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