The ebb and flow of attention: Between-subject variation in intrinsic connectivity and cognition associated with the dynamics of ongoing experience

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Abstract

Cognition is dynamic, allowing us the flexibility to shift focus from different aspects of the environment, or between internally- and externally-oriented trains of thought. Although we understand how individuals switch attention across different tasks, the neurocognitive processes that underpin the dynamics of less constrained elements of cognition are less well understood. To explore this issue, we developed a paradigm in which participants intermittently responded to external events across two conditions that systematically vary in their need for updating working memory based on information in the external environment. This paradigm distinguishes the influences on cognition that emerge because of demands placed by the task (sustained) from changes that result from the time elapsed since the last task response (transient). We used experience sampling to identify dynamic changes in ongoing cognition in this paradigm, and related between subject variation in these measures to variations in the intrinsic organisation of large-scale brain networks. We found systems important for attention were involved in the regulation of off-task thought. Coupling between the ventral attention network and regions of primary motor cortex was stronger for individuals who were able to regulate off-task thought in line with the demands of the task. This pattern of coupling was linked to greater task-related thought when environmental demands were high and elevated off-task thought when demands were low. In contrast, the coupling of the dorsal attention network with a region of lateral visual cortex was stronger for individuals for whom off-task thoughts transiently increased with the time since responding to the external world increased. This pattern is consistent with a role for this system in the time-limited top-down biasing of visual processing to increase behavioural efficiency. Unlike the attention networks, coupling between regions of the default mode network and dorsal occipital cortex was weaker for individuals for whom the level of detail decreased with the passage of time when the external task did not require continuous monitoring of external information. These data provide novel evidence for how neural systems vary across subjects and may be underpin individual variation in the dynamics of thought, linking attention systems to the maintenance of task-relevant information, and the default mode network to supporting experiences with vivid detail.

Highlights

We explored between-subject variation in the neural correlates of ongoing thought

The connectivity of attention networks was linked to the dynamics of off-task thought

The ventral attention network was linked to sustained changes in off-task thought

The dorsal attention network was linked to transient changes in off-task thought

Default mode network connectivity was linked to levels of detail in ongoing thought

Introduction

Since the earliest psychological investigation, cognition has been argued to be dynamic, exemplified by William James' (James, 1892) characterization of consciousness as a stream or river a famous example. The dynamics of cognition are reflected in our ability to switch between external tasks; however, they also manifest when we shift from external to internal modes of mental operations, such as when we start considering professional problems on the commute to work, or imagine a holiday while washing dishes. Psychological investigations reveal that internal modes of thought are common (Killingsworth & Gilbert, 2010), and cognitive neuroscience has demonstrated that when unoccupied by a task, brain activity has complex temporal dynamics (Hutchison, Womelsdorf, Gati, Everling, & Menon, 2013), some of which may reflect patterns of ongoing thought (Christoff, Gordon, Smallwood, Smith, & Schooler, 2009). Patterns of neural activity calculated through their neural dynamics at rest also relate to behaviours such as intelligence and creativity (Beaty et al., 2018; Finn et al., 2015; Wang et al., 2017). Converging neurocognitive evidence, therefore, highlight that dynamical changes in patterns of ongoing cognition are an important element of human mental life.

Although we understand how changes between tasks can occur reasonably well (Monsell, 2003), we know less about the temporal transitions in relatively unconstrained cognitive states. To address this gap in the literature, we conducted a between subject investigation to describe the dynamics of patterns of thoughts in the laboratory. Our study capitalises on the fact that when external demands are low, people often devote time to thinking about matters unrelated to events in the here-and-now (Teasdale et al., 1995) and that this tendency increases the longer people spend in these undemanding circumstances (Smallwood, Obonsawin, & Reid, 2002). Experience sampling allows descriptions of experience at different moments in time to be generated (Smallwood & Schooler, 2015), providing a tractable way to gain insight into how cognition is organised, even in the absence of a complex external task. Our study also builds on recent evidence (Gratton et al., 2018) which suggests that functional connectivity calculated at rest reflects a stable fingerprint of individual differences (Finn et al., 2015). Moreover, metrics defined from the resting state have been successfully used to predict a range of measures of individual variation as measured outside of the scanner including well-being (Smith et al., 2015) and psychiatric conditions (Kernbach et al., 2018; Lefort-Besnard et al., 2018), as well as more detailed measures of cognition including intelligence (Finn et al., 2015), meta-cognition (Baird, Smallwood, Gorgolewski, & Margulies, 2013), bi-stable perception (Baker, Karapanagiotidis, Coggan, Wailes-Newson, & Smallwood, 2015), cognitive flexibility (Vatansever, Manktelow, Sahakian, Menon, & Stamatakis, 2016), attention (Rosenberg et al., 2016), and creativity (Beaty et al., 2018).

Our study brings together these two approaches to examine whether between subject variation in patterns of ongoing thought can be linked to variation in the intrinsic organisation of neural function as assessed at rest. In a large sample of individuals we used experience sampling to determine the temporal profile of different patterns of ongoing thought in the lab. We also described these individuals in terms of their performance on well-established measures of cognitive function including creativity, fluid intelligence, and cognitive flexibility. Finally, using resting state functional magnetic resonance imaging (fMRI) we measured the organisation of neural function in the same individuals using functional connectivity analyses (Biswal, Zerrin Yetkin, Haughton, & Hyde, 1995). Using these data we conduct a sequence of between subject analyses. First, we explore the association across individuals between metrics that describe temporal patterns of ongoing thought with lab measures of performance on cognitive tasks. Second, we examined whether between-subject variation in the patterns of ongoing thought are linked to intrinsic neural organisation measured during periods of wakeful rest. Although our between subject design cannot provide a description of the neural processes that contribute to momentary changes in ongoing thought, it can provide information on how experiential, cognitive, and neural measures vary together across individuals. Building on the growing tradition of linking between subject variation in cognition to variation in neural function reviewed above, our study hoped to exploit individual differences to examine the neural and correlates of dynamic patterns of ongoing thought.

Studies from cognitive neuroscience highlight a number of candidate large-scale networks likely to be important for temporal variation in patterns of ongoing thought (Christoff, Irving, Fox, Spreng, & Andrews-Hanna, 2016; Golchert et al., 2017; Hasenkamp, Wilson-Mendenhall, Duncan, & Barsalou, 2012; Kucyi, 2017; Smallwood et al., 2016). For example, the dorsal attention network involves regions of lateral parietal, occipital, and frontal cortex (Fox, Corbetta, Snyder, Vincent, & Raichle, 2006) and is important when top-down attention biases visual input to facilitate efficient subsequent behaviour (Corbetta & Shulman, 2002; Wen, Yao, Liu, & Ding, 2012). Regions largely overlapping with this network have also shown to be active during both visual and working memory search (Kuo, Nobre, Scerif, & Astle, 2016), making it likely that it will play a role in regulating ongoing thought during tasks that engage these processes. The ventral attention network, on the other hand, includes regions of anterior insula and anterior cingulate cortex, temporparietal junction, and ventral lateral prefrontal regions (Fox et al., 2006). This plays a general role in controlling the focus of attention by emphasising information salient to a given situation (Asplund, Todd, Snyder, & Marois, 2010; Dosenbach et al., 2006). Given both ventral and dorsal attention networks play prominent roles in facilitating external task-relevant behaviour (Vossel, Weidner, Driver, Friston, & Fink, 2012), it seems plausible that they will play a role in the dynamics of ongoing thought as they emerge during a laboratory task.

In addition to attention systems, transmodal regions of cortex are likely to be important for patterns of ongoing thought. The fronto-parietal network, including the inferior frontal sulcus and the intraparietal junction (Vincent, Kahn, Snyder, Raichle, & Buckner, 2008), is recruited across task domains whenever cognitive demands increase (Klingberg, O'Sullivan, & Roland, 1997) and is important for allowing cognition to proceed flexibly along a set of abstract rules (Cole et al., 2013). Given its role in demanding tasks this system could be important for maintaining a content-dependent attentional set that is important for a particular task (Slagter et al., 2007; Spreng, Sepulcre, Turner, Stevens, & Schacter, 2013), particularly in demanding task conditions. Another transmodal system, the default mode network, is also believed to be important for ongoing cognition (Christoff et al., 2009; Gerlach, Spreng, Gilmore, & Schacter, 2011; Kucyi & Davis, 2014; Mooneyham et al., 2017; Smallwood, Brown, Baird, & Schooler, 2012; Smallwood et al., 2016; Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010). This network entails posterior and anterior regions of medial frontal and cingulate cortex (Greicius, Krasnow, Reiss, & Menon, 2003), as well as lateral regions in the temporal lobe, and was first identified through its tendency to decrease in activity when participants perform complex externally demanding tasks (Raichle et al., 2001; Shulman et al., 1997).

More recent investigations have shown that activity in this system increases when ongoing thought depends to a greater extent on internally represented information (Konishi, McLaren, Engen, & Smallwood, 2015; Murphy et al., 2018; Vatansever, Menon, & Stamatakis, 2017). These states of memory guided thought include periods of off-task thought (Christoff et al., 2009), imagining the future (Østby et al., 2012; Spreng & Grady, 2010), as well as social problem solving and planning (Gerlach et al., 2011; Mars et al., 2012). Contemporary accounts of the default mode network argue that its apparent role in multiple different cognitive states may emerge from its position at the top of a functional hierarchy that is maximally distant from sensory input (Margulies et al., 2016). This hierarchical organization would allow regions of the default mode network to contribute to a wide range of cognitive states, including tasks, through its capacity to flexibly couple with other networks in a situation-dependent manner (Mooneyham et al., 2017).

Study outline

We measured ongoing thought in a simple task in a sample of 157 individuals in the behavioural laboratory. Their task was to make intermittent decisions about the location of shapes (squares, triangles and circles, see Figure 1). We manipulated two aspects of this task. First, we varied the elapsed time between these decisions, randomly from approximately three to eighteen seconds, hypothesising that longer elapsed time intervals would provide more opportunity for ongoing cognition to evolve. By sampling experience across this period, therefore, we hoped to determine the temporal profile that different patterns of thought have. We refer to the changes in cognition that emerge due to elapsed time as *transient*. Second, we manipulated whether the task required continuous monitoring of the external environment using an alternating block design. In one condition, which we refer to as 0-back, participants made visuospatial decisions using information available at that moment in time. This meant that large periods of this task had minimal task demands, providing a context that allows cognition to evolve in a relatively unconstrained fashion. In a second condition, which we refer to as 1-back, similar decisions were made using information presented on the prior trial. The reliance on prior information means that the 1-back condition requires a continuous monitoring of external input in order to perform the task accurately. This manipulation allows us to determine if continuous demands of the environment constrain the dynamics of ongoing thought.

We refer to changes in experience that emerge because of the nature of the ongoing task as *sustained*.

In our study, the same individuals also participated in a resting state fMRI session providing the opportunity to understand how variations in temporal patterns of cognition across individuals within our task relate to their underlying neural architecture. They also performed a battery of tests to describe their aptitude in a range of cognitive domains. Studies from psychology have shown that patterns of ongoing cognition have a complex relationship to measures of cognitive function. For example, off-task experiences interfere with external task performance (Reason, 1990; Smallwood, Beach, Schooler, & Handy, 2008; Smallwood et al., 2004), and individuals with poor attentional control (Franklin et al., 2017; Seli, Smallwood, Cheyne, & Smilek, 2015), or low fluid intelligence (Mrazek et al., 2012), tend to have problems preventing these experiences from detrimentally impacting on ongoing performance (Kane et al., 2007; McVay & Kane, 2012; McVay, Kane, & Kwapil, 2009; Mrazek, Franklin, Phillips, Baird, & Schooler, 2013). On the other hand, off-task experiences have been linked to better creativity (Baird et al., 2012; Wang et al., 2017), social problem solving (Ruby, Smallwood, Sackur, & Singer, 2013), and planning (Baird, Smallwood, & Schooler, 2011; McMillan, Kaufman, & Singer, 2013). It is hypothesised that this class of associations reflect the shared role that generative processes play both in acts of creative problem solving, and in the production of cognition in the absence of an external stimulus (Smallwood & Schooler, 2015). To capture these patterns of associations we selected three measures from the battery of tasks that these participants completed (i) The Unusual Uses Task (UUT) (Guilford, 1967), to measure creativity; (ii) Raven’s progressive matrices (RAPM) (Raven, 1994), to provide a measure of fluid intelligence; and (iii) Task Switching (Mayr & Keele, 2000) to provide a measure of flexibility.

Using these measures we conducted a series of between-subject analyses to identify neurocognitive patterns associated with changes in patterns of ongoing thought. First, we determined patterns of individual variation in how ongoing experience varies with demands imposed by the task, the passage of time, and a combination of both factors. We expected based on prior studies that off task thought will increase with elapsed time in non-demanding tasks, and this relationship is attenuated in tasks with greater task demands (Smallwood et al., 2002). We also examined whether these changes in thought have a relationship to the selected measures of creativity, flexibility, and fluid intelligence. This step helps characterise between subject variation in how temporal changes in ongoing thought identified in our study relate to different well-established components of cognition (creativity, intelligence, and flexibility). Next, we performed our main analysis - a sequence of functional connectivity analyses to examine how between subject variation in the temporal patterns of ongoing thought are related to individual variation in the organisation of the cortex. We focused on four large-scale systems: the ventral attention network, the dorsal attention network, the fronto-parietal network, and the default mode network. For each network we performed a group level regression to determine regions of cortex whose correlation with the time series of the network varied across individuals with respect to different temporal patterns of ongoing thought. This analytical step characterises temporal changes in ongoing thought in terms of their associations with the underlying neural architecture.

Using these data our study aimed to shed light on several issues that are important for contemporary accounts of ongoing thought (Christoff et al., 2016; Smallwood & Schooler, 2015). One important question is how attention is maintained on task relevant information. Prominent accounts have argued that the default mode network is important for task negative states given its pattern of deactivation during tasks (Raichle et al., 2001), its negative relationship to task positive systems (Fox et al., 2005), its associations with worse task performance (Smallwood et al., 2013; Weissman, Roberts, Visscher, & Woldorff, 2006), and elevated activity during periods of off task thought (Allen et al., 2013, Christoff et al., 2009). An alternative view is that task related cognition is maintained through the integrity of attentional processes (McVay & Kane, 2010). Neuroscience has shown that maintaining attention on complex demanding tasks depends on a combination of multiple networks including the ventral and dorsal attention networks and the frontoparietal control network (Duncan, 2010). Previously we had found that a focus on current concerns at rest was linked to reduced connectivity within large scale attention systems and poor performance on measures of intelligence (Wang et al., 2018). We hoped our study would illuminate whether between subject variation in either sustained or transient aspects of the ability to attend to a task is better accounted for by the functional organisation of the default mode, or, the attention and control networks. A second question is the extent to which the influences on patterns of ongoing thought vary across contexts. Although initial work assumed that patterns of ongoing thought were independent of context, growing evidence suggests that they may vary with the momentary demands posed by the external environment (Smallwood & Andrews-Hanna, 2013). Accordingly, we hoped to identify whether variations in patterns of ongoing thought in the different task contexts (0 back and 1 back) were linked to similar or different underlying neurocognitive traits.

Methods

Participants

A group of 157 participants (95 females; mean age=20.43, SD=2.63 years) were recruited for this study. They were right handed, native English speakers, with normal/corrected vision, and no history of psychiatric or neurological illness. This cohort was acquired from the undergraduate and postgraduate student body at the University of York. All volunteers provided informed written consent and received monetary compensation or course credit for their participation.

Procedure

In the scanner, participants completed a 9-minute eyes-open resting-state scan during which there was a fixation cross on-screen. There were no written instructions for this scan, but participants were verbally instructed to look at the fixation cross and try not to sleep. Following the imaging protocol, participants took part in a comprehensive set of behavioural assessments that captured different aspects of cognition, including the tasks to measure component processes, and those used to measure mind-wandering. The tasks were completed over three 2-hour long sessions on different days, with the order of sessions counterbalanced across participants.

Experiential assessment

We measured ongoing cognition in a paradigm that alternated between blocks of 0-back and 1-back decisions manipulating memory load (see Figure 1). Non-target trials in both 0-back and 1-back conditions were identical, consisting of black shapes (circles, squares or triangles) separated by a line, the colour of which signified whether the condition was 0-back or 1-back (mean presentation duration = 1050 ms, 200 ms jitter). The initial block was counterbalanced across individuals. The non-target trials were followed by presentation of a black fixation cross (mean presentation duration = 1530 ms, 130 ms jitter). Non-targets were presented in runs of between 2 and 8 with a mean of 5 following which a target trial or a multidimensional experience sampling (MDES) probe was presented. In both 0-back and 1-back non-target trials, participants were not required to make a behavioural response. In the 1-back trials, participants had to maintain the visuo-spatial array in

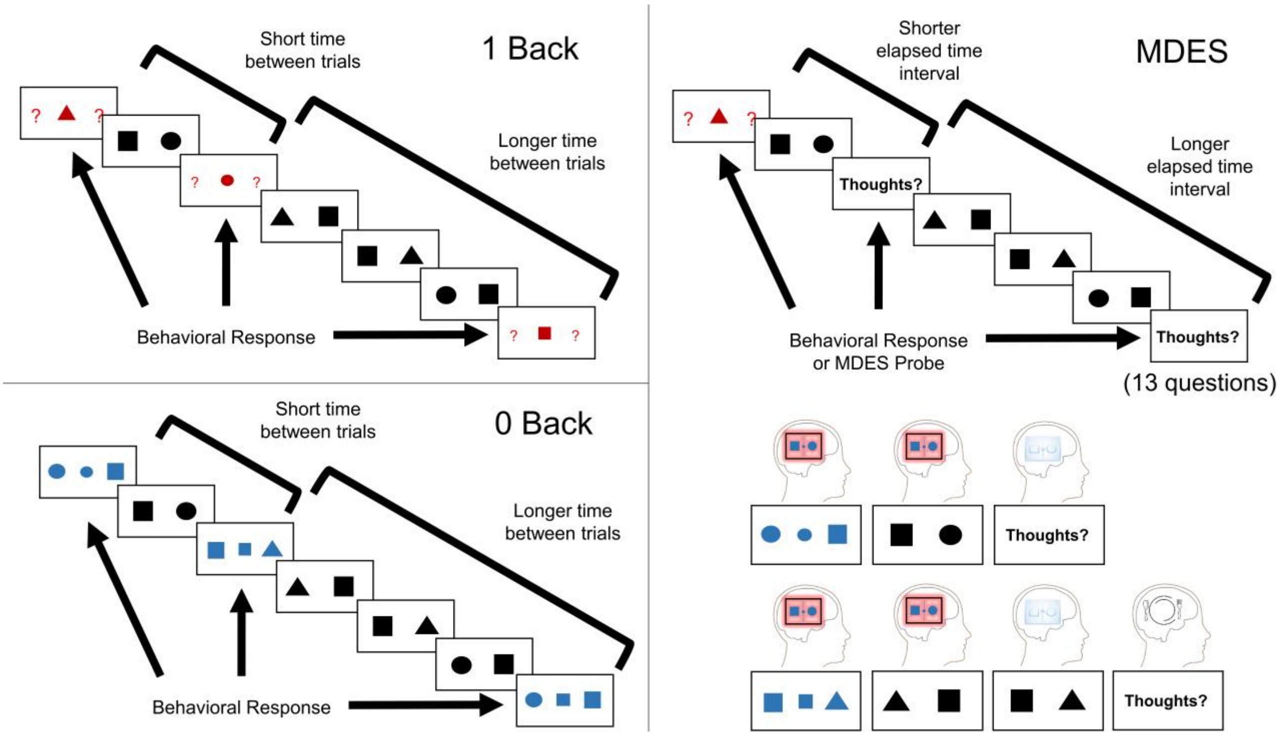

Figure 1. Ongoing thought was measured during blocks of alternating 1-back (top left) and 0-back (bottom left) tasks. During target trials individuals had to state the location of the centre shape in either the on-screen trial (0-back) or the preceding trial (1-back). The condition was denoted by the colour of the centre line and the shapes in the target trial. During task performance, the target trials either required a decision based on the location of the shape, or were replaced by a multidimensional experience sampling probe (top right). These were used to assess ongoing cognition and consisted of 13 questions about the participant’s thoughts while they performed the task (e.g. bottom right). The time between target trials (or target trials and thought probes) varied and this variation was leveraged to analyse the effect of elapsed time since a target trial on participants’ thought content.

working memory for each trial and use this information appropriately in the target trials. In the 0-back trials there was no need to retain the details of the non-target trials since the response trials could be completed based on the information in the trial, releasing working memory from task relevant information. The task was performed on three separate days in sessions that lasted around 25 minutes, and this was separated into 8 blocks. The short session length was chosen to minimise time-on-task effects that have been shown to emerge as testing sessions extend beyond approximately 25 minutes (McVay & Kane, 2009). These effects were also expected to be limited in our task due to the low overall working memory load (Helton & Russell, 2011).

During target trials, participants were required to make a response, and this response differed depending on condition. In the 0-back condition, the target trial was a pair of coloured shapes presented either side of a coloured line with a probe shape in the centre of the screen at the top. Participants had to press a button to indicate whether the central shape matched the shape on the left or right hand side of the screen. In the 1-back condition, the target trial consisted of two coloured question marks presented either side of a coloured line with a probe shape in the centre of the screen. Participants had to indicate via button press whether the central shape matched either the shape on the left or right side of the screen on the previous (non-target) trial. This task is presented schematically in Figure 1.

The contents of on-going thought during the 0/1-back task was measured using multidimensional experience sampling (MDES). On each occasion participants were asked about their thoughts, they answered the 13 questions presented in Table 1. Participants always rated their level of task focus first and then described their thoughts at the moment before the probe on a further 12 dimensions. MDES probes occurred on a quasi-random basis to minimise the likelihood that participants could anticipate the occurrence of a probe. At the end of each run participants were either probed with a target or on 20% of the time a MDES probe occurred. Since it was possible that two MDES probes could occur in succession, we only examined the MDES probes when the previous behavioural event was a target trial. This ensured that the effects of elapsed time only reflected changes that took place since participants made a response to a target, and did not include changes taking place after participants completed a MDES probe.

Table 1: Experience sampling questions

Dimensions	Questions	1	4
Task	My thoughts were focused on the task I was performing.	Not at all	Completely
Future	My thoughts involved future events.	Not at all	Completely
Past	My thoughts involved past events.	Not at all	Completely
Self	My thoughts involved myself.	Not at all	Completely
Person	My thoughts involved other people.	Not at all	Completely
Emotion	The content of my thoughts was:	Negative	Positive
Images	My thoughts were in the form of images.	Not at all	Completely
Words	My thoughts were in the form of words.	Not at all	Completely
Vivid	My thoughts were vivid as if I was there.	Not at all	Completely
Specific	My thoughts were detailed and specific.	Not at all	Completely
Habit	This thought has recurrent themes similar to those I have had before.	Not at all	Completely
Evolving	My thoughts tended to evolve in a series of steps.	Not at all	Completely
Deliberate	My thoughts were:	Spontaneous	Deliberate

In total an average of 30.7 (*SD* = 5.7, range: 34) MDES probes occurred; in the 0-back condition an average of 15.4 (*SD* = 3.6, range: 22) and in the 1-back condition an average of 15.4 (*SD* = 3.2, range: 18) occurred. These probes occurred between 3.4 and 17.8 seconds following a target trial/switching event (mean = 10.5s, *SD* = 3.5s). The quasi-random nature of the probe timing meant that they were distributed randomly arranged around 6 evenly spread time points. To match the distribution of the probes and ensure the majority of participants had at least one probe at each time point, the probes were divided into 3 bins (3.4-7.5, 7.5-12.6, and 12.6-17.8 seconds) that were used for all analyses. This allowed our analyses to focus on relatively stable measures of patterns of ongoing thought at each elapsed time interval. The mean number of experience sampling probes per bin were: 7.14 (*SD* = 2.85), 14.11 (*SD* = 3.75), and 9.49 (*SD* = 3.18), respectively.

For the purpose of analyses the scores on the 13 mind wandering questions were entered into a principal component analysis (PCA) to describe the underlying structure of the participants responses. Following prior studies (Konishi, Brown, Battaglini, & Smallwood, 2017; Medea et al., 2016; Ruby, Smallwood, Engen, & Singer, 2013) we concatenated the responses of each participant in each task into a single matrix and employed a principal components reduction with varimax rotation. We selected the number of components based on the scree plot.

Tasks

The behavioural tasks were allocated into three sessions based on apparatus needed. Visual attention and generative semantic tasks were in session A, and semantic and episodic memory tasks were in session B and C. In each session, the first and second tasks were the mind-wandering task and the flanker task. In session B and C, the third task was the encoding and the delayed-recall phases of the word pair memory task respectively. The rest of the tasks were performed based on a pre-allocated order.

General apparatus of the laboratory session

In session B and C, the participants were in a sound proofed booth with a big glass window for the testers to monitor them. There were four testing spaces separated by office screen dividers. The tasks were delivered on Windows 7 computers and presented on 21 inches LCD monitors. Headsets were given to participants to deliver audio stimulus and blocking distracting noises. Participants were instructed to view the screen from a distance of 65 cm. The participants raised their hand to inform the experimenter to start each task. In session A, the visual attention tasks were delivered on a Windows 7 computer and presented on a 21 inches CRT monitor in a small room with light switch. The generative semantic tasks were delivered on a Windows 7 computer and presented on a 21 inches LCD monitor and a headset with microphone attached were used to recording verbal responses.

The tasks included in the analysis of this study were:

1. Task-switching task.
2. Raven's advanced progressive matrices.
3. Unusual uses task.

Task-switching task

We used the task-switching paradigm developed by (Mayr & Keele, 2000) and the design and task materials were constructed based on (Whitmer & Banich, 2007) in Psychopy (Peirce, 2007). This task measured executive control on inhibiting previously relevant information. In this task, the participant identified the spatial location of a deviant object with a verbal instruction cue. The participant used a number pad to respond. Number 1,2,4, and 5 were used. Each of them responded to the spatial location of the designated rectangle. In each trial, four blue rectangles arranged into a two-by-two matrix were displayed on screen. The rectangles can vary from each other on one of three dimensions: size, motion, or orientation. Before a set time interval of 100ms or 900ms, a verbal cue identifying the dimension appeared on the centre of the screen. There were one practice block and two experiment blocks. The cue-stimuli interval in the practice is 500 msec, and 900 msec and 100 msec respectively in the two experiment blocks. The trials are categorised into four: control, inhibitory, uncategorised switch, and repeat.

Inhibitory trials are those in which the cue is different from the cue in the immediately preceding trial but the same as that two trials back (e.g. size-motion-**size**). When a subject switches from one task set to another, the first task set is inhibited to allow a faster transition. Therefore, returning to the inhibited task immediately requires overcoming this inhibition and takes more time. Control trials are those in which the cues in the trial, the previous trial, and two trials back, are all different (e.g. size-motion-**orientation**). In these trials the set has been abandoned less recently and there is less inhibition to overcome. An individual's ability to inhibit previously held information is therefore defined as inhibition trial reaction time minus control trial reaction time. An inability to inhibit a previous task set results in a smaller time cost as there is less inhibition to overcome, and the task set from two trials previously can be accessed easily as it was not successfully inhibited completely during the previous trial. In this way a high inhibition score represents greater executive ability in inhibiting previously relevant information.

Set switching cost is the additional time it takes to respond to non-inhibitory trials that involve a switch of task compared to those that are a repeat (e.g. size/orientation-orientation-**motion** minus any-size-**size**). These costs reflect the time it takes to flexibly reconfigure the task representations and a higher score means an individual has a lower executive ability to perform these processes.

Raven’s advanced progressive matrices

The Ravens Advanced Progressive Matrices (Raven, 1994) measured ‘fluid intelligence’ – that is the ability to make sense and meaning out of complex non-verbal stimuli. In order to complete the task participants were tasked with finding new patterns and relationships between the stimuli. The APM used in the current study contained two tests: (i) practice test - containing 2 problems and (ii) the full test – containing 36 problems. For each problem a set of 9 boxes (ordered in a 3x3 design) were shown on the screen. All but one box contained a pattern. At the bottom of the screen were 4 additional boxes, each containing a unique pattern. Participants were required to select out of these 4 potential boxes which pattern should go in the empty box. During the practice phase participants were given online feedback outlining whether their response was correct and, if not, how they should decide which box was the correct answer. If participants had any further questions, then they were instructed to ask the experimenter before starting the main experiment. During the full test no feedback was given. Participants were given 20 minutes to complete as many problems as they could, the problems got progressively more difficult.

Unusual uses task

The Unusual Uses Task (Guilford, 1967) assessed divergent thinking and creativity. Participants were instructed to list as many unusual uses as they can for a familiar object. Three objects were selected (newspaper, brick, and shoe). Uses were considered ‘unusual’ if they were not the original use of the item. For example, saying ‘crosswords’ for newspaper would not be considered unusual, however saying ‘animal bedding’ would. For each object, the object name appeared on screen for two minutes and participants were required to type as many unusual uses as they could. The total number of unique uses they listed for each item was calculated. Repetition of uses was not included (e.g., saying ‘animal bedding’ and ‘bedding for animal cage’ would only count as one unusual use). The participant’s creativity score was based upon the mean number of unusual uses across the three objects.

Resting state fMRI

Image acquisition

Structural and functional data were acquired using a 3T GE HDx Excite MRI scanner utilising an eight-channel phased array head coil (GE) tuned to 127.4 MHz, at the York Neuroimaging Centre, University of York. Structural MRI acquisition in all participants was based on a T1-weighted 3D fast spoiled gradient echo sequence (TR=7.8 s, TE=minimum full, flip angle=20°, matrix size=256×256, 176 slices, voxel size=1.13×1.13×1 mm). Resting-state activity was recorded from the whole brain using single-shot 2D gradient-echo-planar imaging (TR=3 s, TE=minimum full, flip angle=90°, matrix size=64×64, 60 slices, voxel size=3×3×3 mm^3, 180 volumes). A FLAIR scan with the same orientation as the functional scans was collected to improve co-registration between subject-specific structural and functional scans.

Data pre-processing

Functional and structural data were pre-processed and analysed using FMRIB's Software Library (FSL version 4.1, http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FEAT/). Individual FLAIR and T1 weighted structural brain images were extracted using BET (Brain Extraction Tool). Structural images were linearly registered to the MNI-152 template using FMRIB's Linear Image Registration Tool (FLIRT). The resting state functional data were pre-processed and analysed using the FMRI Expert Analysis Tool (FEAT). The individual subject analysis involved: motion correction using MCFLIRT; slice-timing correction using Fourier space time-series phase-shifting; spatial smoothing using a Gaussian kernel of FWHM 6mm; grand-mean intensity normalisation of the entire 4D dataset by a single multiplicative factor; highpass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma=100 s); Gaussian lowpass temporal filtering, with sigma=2.8 s.

Data analysis

Behavioural

The loadings on each dimension of thought for each of the three time points were entered into a repeated measures Analysis Of Variance (ANOVA), with two factors time (with three levels) and task (with two levels). Scores from the Task-switching, RAPM, and UUT were included as between subject covariates.

Resting state fMRI

We extracted the time series from the ventral attention, dorsal attention, frontoparietal control, and default mode networks (as defined by the Yeo, Krienen et al. (2011) parcellation: see Supplementray Figure 2), and used these as explanatory variables in connectivity analyses at the single subject level. In each analysis, we entered 11 nuisance regressors; the top five principal components extracted from white matter (WM) and cerebrospinal fluid (CSF) masks based on the CompCor method (Behzadi, Restom, Liau, & Liu, 2007), and six head motion parameters.

Only subjects who had at least one probe in each time point for both conditions were analysed in the resting state analysis (n = 141). Following the results of the behavioural analysis, only the first two factors of the PCA were used in this step of the analysis. The PCA scores from each task and time point (as in the behavioural analysis) were entered as regressors in the resting state analysis with contrasts to identify any patterns of thoughts that related to the functional connectivity of the brain networks mentioned above. These contrasts included: main effects, effects of task, linear temporal effects, and time by task effects (an increase in one task and a decrease in the other). Group level maps were thresholded with a cluster forming threshold of $Z>3.1$ at an alpha value of $p<.00625$ to correct for multiple comparisons at the voxel-wise level (Eklund, Nichols, & Knutsson, 2016) and control for the number of network seeds used (4) and the two tailed nature of our comparisons. This analysis was performed with motion as a nuisance regressor at the group level to control for possible spurious relationships with motion (Power, Barnes, Snyder, Schlaggar, & Petersen, 2012). Figures were made using BrainNet Viewer (Xia, Wang, & He, 2013).

Results

Behavioural

Decomposition of the trial-level experience sampling reports using PCA revealed four dimensions of thought (see Figure 2, see Supplementary Figure 1 for the scree plot and Supplementary Table 1 for the Eigenvalues). Consistent with our prior studies we characterised these thoughts (in order of decreasing explained variance) as detailed, off-task, modality of, and emotional thought (Poerio et al., 2017). Our first analysis considers how these components change over time, and whether these changes are related to variation in different underlying cognitive components measured by the selected tasks. We used a repeated measures analysis of variance (ANOVA) in which we included factors of task (0-back / 1-back) and elapsed time (Short, Middle, and Long) as within participant factors. We also included variation in the four task measures (RAPM, UUT, Switching, and Inhibition) as continuous between-participant parameters. All parameters were mean-centred prior to analysis. We modelled the main effects of each explanatory variable as well as the interactions between each component of the task and each individual variable.

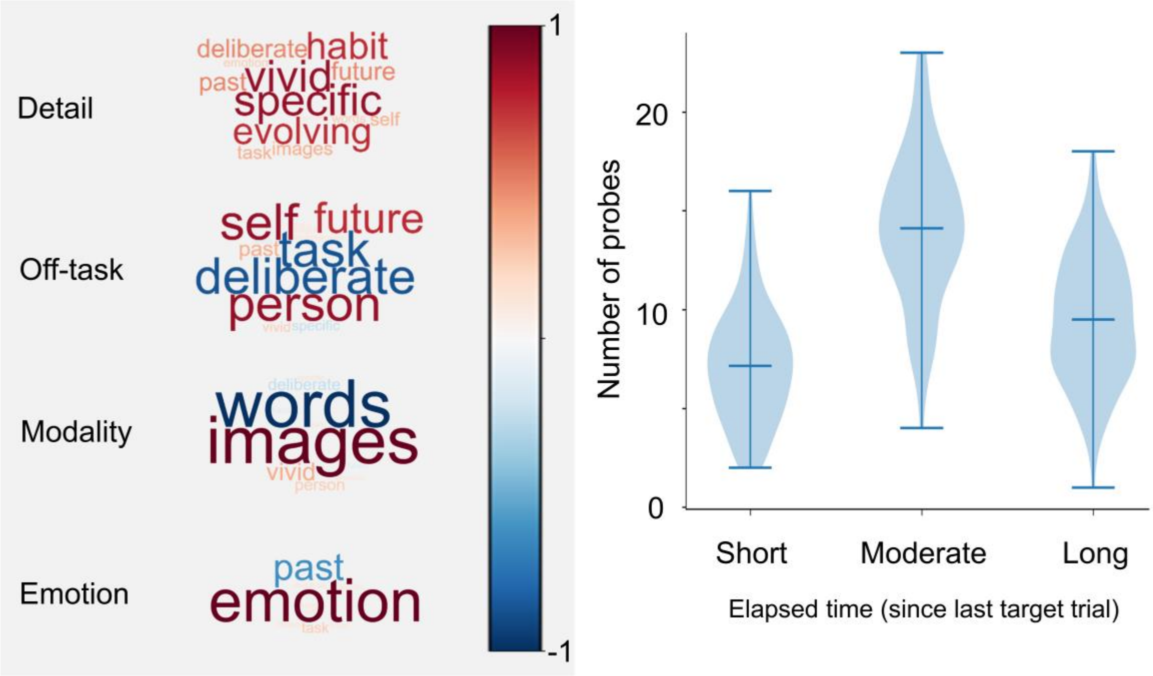

Figure 2. Experience sampling probes revealed four components of thought. Principal Components Analysis applied to the 13 experience sampling questions resulted in four principle components of thought. The wordclouds on the left describe the loadings of each item for these components, with the size representing the magnitude of the loading and the colour the direction of the loading. For example, the question about whether the participant

thought in words loaded strongly and negatively on component 3 (modality), whereas the question for thinking in images loaded strongly and positively. The components were labelled as: Detailed thought, Off-task thought, Modality of thought, and Emotional thought. The violin plot shows the distribution of thought probes across the three time points.

For the off-task component our analysis revealed a significant effect of task (F(2, 129) = 36.650, p <0.001). This effect is presented in Figure 3 (left hand panel) where it can be seen that off-task thinking was greater in the less-demanding task. For this factor there was also a significant interaction between time and inhibition (F (2, 129) = 3.637, p = .028) and task, time, and RAPM (F (2,129) = 5.734, p= .004). Both of these effects are presented in the lower left panel of Figure 3. Individuals who were better able to let go of a prior mental set displayed more on-task thought in the period directly after a target, regardless of the task. In addition, individuals with higher levels of fluid intelligence were associated with an increasing off task focus in the easy task following greater elapsed time.

For detailed thought, there was a main effect of task demands (F (2,129) = 13.772, p<0.001), with more detailed thought in the 1-back task (see upper right hand panel). There were significant interactions between elapsed time and inhibition (F (2,129) = 3.236, p = .041), and a linear contrast of task demands, elapsed time, and UUT (F (1, 129) = 4.300, p = .040). Under non-demanding conditions, higher levels of creativity increased the detail of a person’s thoughts over time within each block. Individuals who were better able to inhibit a prior mental set reported increased levels of detail immediately following a behavioural response.

There was a significant effect of task for the modality of thought (F (2,129) = 13.674, p<0.001), but there were no significant effects or contrasts related to time. The emotional thought component showed no significant effects. Components describing both the task relevance and the level of detail in experience showed patterns of variation over time and so given the interest of this paper in the dynamics of thought we focus our subsequent analyses on these two components. Modality and emotion were not considered further.

Together this analysis suggests that under non-demanding conditions, individuals engage in more off-task thought, and this is potentiated by levels of fluid intelligence - individuals scoring higher on RAPM show an increased tendency to let their thoughts drift to unrelated matters when task demands are low. Under the same situations, thoughts become increasingly detailed for individuals who shower greater creativity. In contrast, the ability to inhibit a previously-relevant mental set is linked to changes in experience following a period of task-relevant action, with ongoing thought relatively on-task, but less detailed during longer blocks.

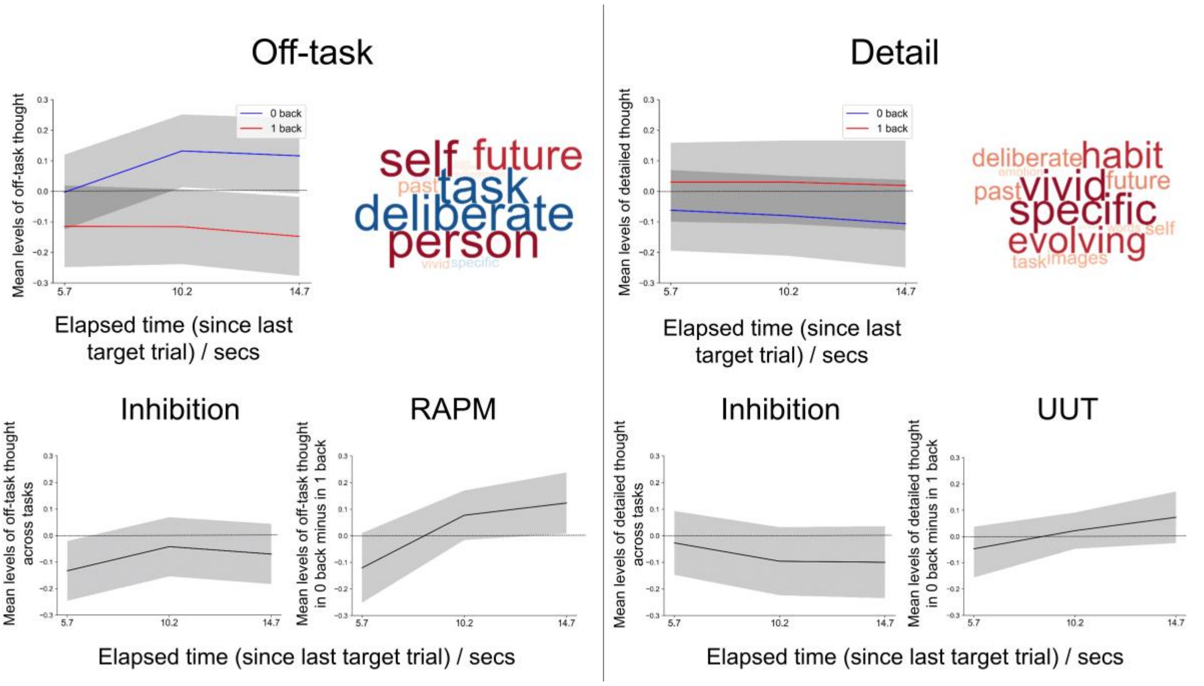

Figure 3. Relationship between elapsed time, task, and components of cognition (creativity, fluid intelligence, and flexibility) and patterns of ongoing thought (n = 157). Off-task thought showed greater increases with time under non-demanding conditions dependent on fluid intelligence. Detailed thought showed greater increases with time in the non-demanding task dependent on increased creativity. We also found that the ability to disregard a mental set was linked to more on task and less detailed experiences following a task relevant response. The top half of the figure shows estimated marginal means produced by our analysis, with the bottom half showing parameter estimates for the relevant contrasts (mean scores across both tasks for time effects, and 0-back minus 1-back subtractions for time by task interactions). The shaded areas indicate the upper and lower 95% Confidence Intervals.

Resting state fMRI

Next, we performed a series of group-level whole brain resting-state functional connectivity analyses to understand the intrinsic architecture that underpins variations in ongoing cognition across tasks and time. We focused on two components that were significant in the behavioural analyses (Detail and Off-task thought) including their mean-centred loadings for each component for each temporal interval for each task (a total of 12 variables of interest). Using these scores we formalised contrasts that corresponded to variations in the factor of our design (sustained and transient). For each component we contrasted mean differences across the task, linear increases and decreases with time, and the interaction of these two factors. Four seeds were used in 4 separate whole brain analyses: the dorsal and ventral attention networks, the frontoparietal network, and the default mode network, all taken from the seven network Yeo parcellation (Yeo et al., 2011). In this parcellation the default mode network includes the posterior cingulate cortex, the medial pre-frontal cortex, the angular gyrus, and the middle temporal gyrus in the temporal lobe. The fronto-parietal network involves bilateral dorsal lateral prefrontal cortex, intraparietal sulcus and posterior temporal cortex, as well as the pre supplementary motor area, and dorsal posterior medial cortex. The ventral attention network includes bilateral regions of dorsal prefrontal cortex, anterior insula, anterior cingulate cortex, and the tempo-parietal junction. The dorsal attention network includes regions both anterior and posterior to the central sulcus, dorsal lateral parietal cortex, and lateral occipital cortex. Please note the spatial distribution of these networks are also presented visually in the relevant figures and in Supplementary Figure S2. Following Eklund et al., these results were cluster thresholded at Z>3.1 (Eklund et al., 2016) and we corrected the alpha value for the number of comparisons we made (four models and two tailed tests equals 8 comparisons, p = .00625). All results that passed cluster correction at Z>3.1, p<.05 (two-tailed) are shown in Supplementary Table 2.

All maps included in this paper are uploaded to Neurovault in the collection: The ebb and flow of attention (https://neurovault.org/collections/3725/).

Dorsal and ventral attention networks

Figure 4 shows the results from the models that used attention networks as seeds (see right upper sub panel for the spatial distribution of these networks). We identified a significant between subject association between connectivity from the dorsal attention network to the left lateral occipital cortex and a linear increase in off-task thoughts with elapsed time. In order to visualise this relationship, the participants were split by the strength of this connectivity and their off-task thought scores were plotted over time (averaged across the two tasks, see bottom left of Figure 4). It is clear that connectivity between the dorsal attention network and this lateral region of occipital cortex discriminated participants in terms of their likelihood for off-task thought in longer elapsed time durations, and did not discriminate in shorter intervals. By correlating the degree of connectivity between these regions and cognitive measures we identified a significant correlation with both RAPM (r(139)=.189, p=.025) and UUT (r(139)=.237, p=.005) scores (see Figure 5). This pattern of increasing off-task thought over time matches the relationship between reports of off-task experience in our previous behavioural analysis. However, the relationship to task behaviour was specific to the easy task, while the link between dynamics and the connectivity of the dorsal attention network was independent of the task.

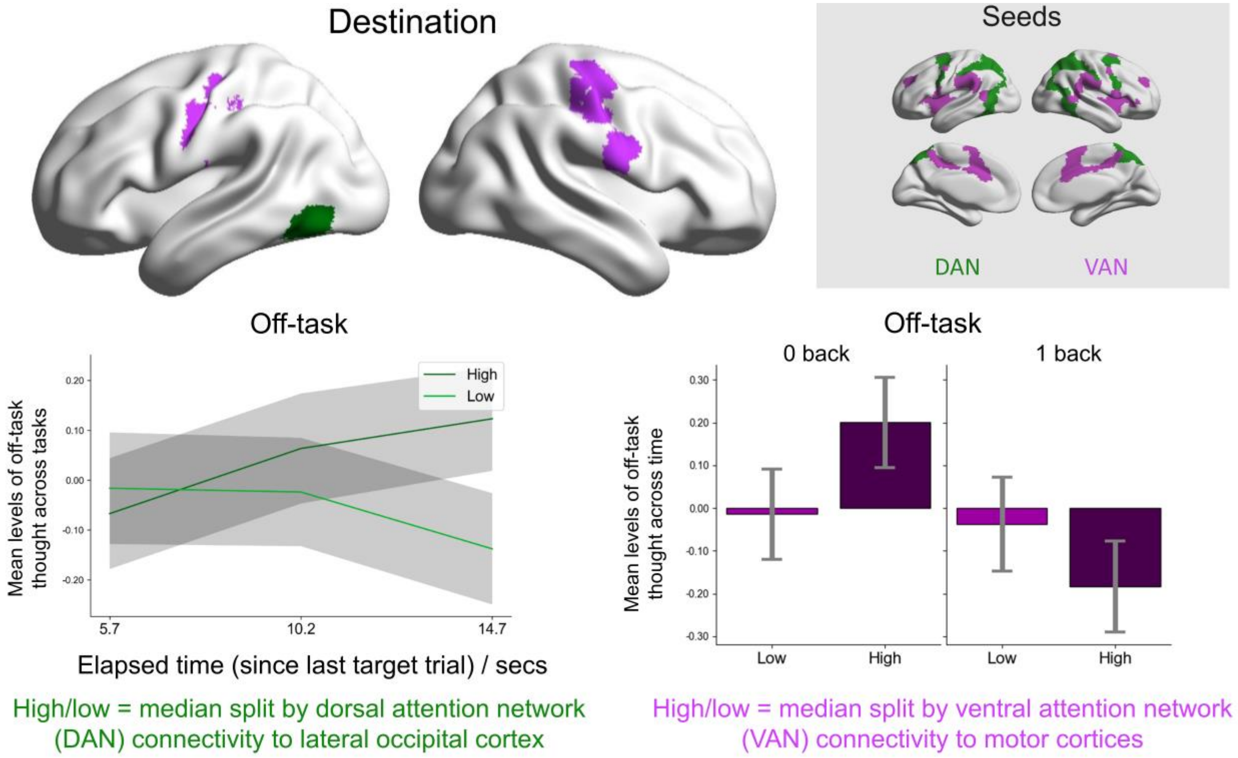

Figure 4. Group level regression using off-task PCA scores as regressors of interest revealed significant clusters for both ventral and dorsal attention networks (n=141). A significant cluster in the left lateral occipital cortex displayed connectivity that related to an increasing pattern of off-task thought over time. The mean off-task score across the tasks was split into a high and low connectivity group and plotted against time (bottom left). Two significant clusters in bilateral motor cortices displayed connectivity to the ventral attention network that related to more off-task thought in the 0-back task compared to the 1-back. The mean off-task score across time was split into a high and low connectivity group and plotted over the two tasks (bottom right). All analyses were performed using FLAME and had a cluster forming threshold of Z = 3.1 and were corrected both using FWE and to account for both the two tailed nature of our analyses and the number of models performed. The shaded areas indicate the upper and lower 95% Confidence Intervals.

Seeding the ventral attention network revealed a significant between subject association between connectivity to bilateral motor cortices and greater off-task thought in the 0-back than 1-back conditions. To understand this relationship, we split participants on the basis of this connectivity and plotted their average degree of off-task thought in each task (see the bottom right of Figure 4). Individuals with higher connectivity between the ventral attention network and motor cortex demonstrated increased off-task thought in the 0-back task and more on-task thought in the difficult 1-back task. This connectivity was not significantly correlated with any of the cognitive measures (Inhibition: r(139)=.008, p=.923, Switchcost: r(139)=.109, p=.196, RAPM: r(139)=.142, p=.094, UUT: r(139)=.043, p=.611). The ability to constrain off task thought to easier tasks is known as context regulation (Smallwood & Andrews-Hanna, 2013) and is thought to help limit the consequences for poor task performance. To test this relationship we correlated this pattern of connectivity with accuracy on both the 0-back and 1-back tasks. We found a significant correlation with mean task accuracy (r(139)=.183, p=.03). This corresponded to weak correlations of r(139)=.167 (p=.047) and r(139)=.165 (p=.051) in the 0-back and 1-back tasks, respectively. We found no correlation with response time in either task (CRT: r(139)=-.109, p=.20; WM: r(139)=-.050, p=.56; Mean: r(139)=-.084, p=.32). This suggests that the pattern of brain activity associated with better context regulation in terms of ongoing thought was matched by more accurate performance.

Fronto-parietal and default mode networks

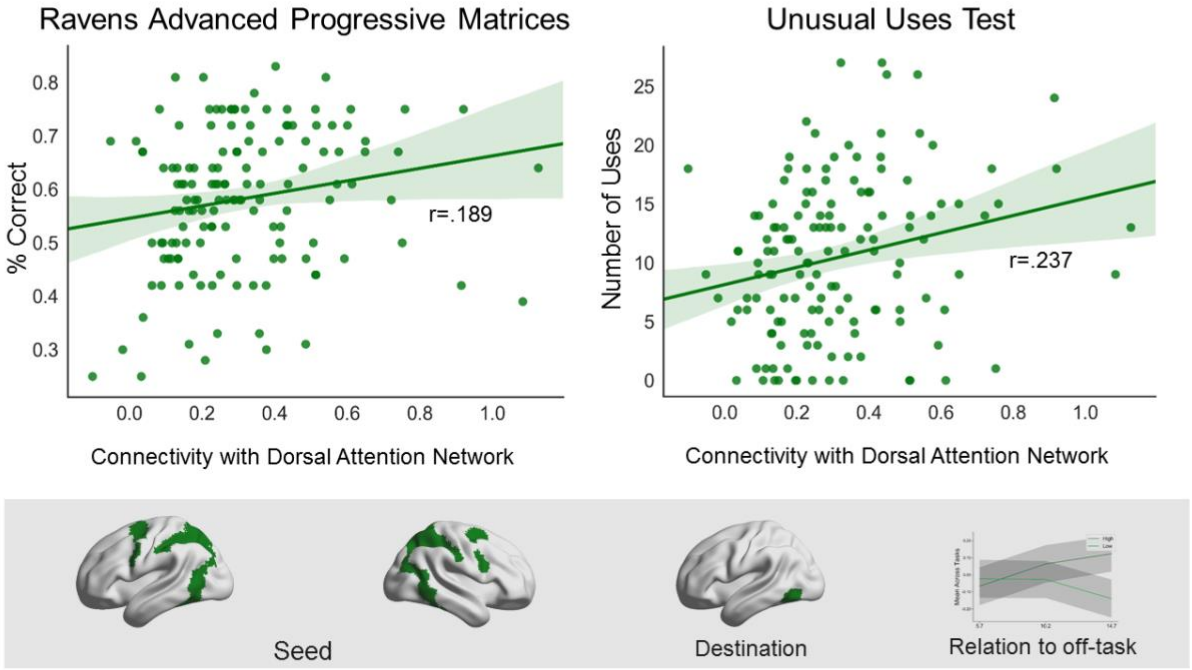

Figure 5. Correlation analysis identified significant relationships between the connectivity of the left lateral occipital cortex and dorsal attention network, identified through an analysis of patterns of ongoing thought, and measures of fluid intelligence and creativity (n=141). The connectivity of this region to the dorsal attention network is plotted against scores from Raven's Progressive Matrices (left) and the Unusual Uses Task (right).

Our next analysis considers the relationship between the intrinsic architecture of regions of transmodal cortex and changes in on-going cognition. Connectivity between the default mode network and a cluster in bilateral lateral visual cortices showed a between subject association that linked level of detail, elapsed time, and the level of task difficulty. As can be seen in the right hand panel of Figure 6 splitting individuals into high and low groups based on this pattern of connectivity revealed that low levels of coupling with vision was associated with a greater differences in detail between the tasks in longer elapsed time intervals. A more detailed visualisation of this effect is presented in the lower right sub panel of Figure 6 where it can be seen that higher levels of temporal correlation between the default mode network and this region of occipital cortex was linked to high detail across conditions, while lower temporal correlation was linked to a reduction in how detailed experience was especially in longer elapsed time intervals in the easier 0-back task.

Analysis for the fronto-parietal network failed to identify any results that reached the alpha level that corrected for the number of models. However, the same contrast between detail and elapsed time and task difficulty that was significant for the default mode network was at trend level for the fronto-parietal network (Z = 3.1, p = .0070, FWE whole brain corrected). Furthermore, visual inspection of this effect indicated that it overlapped with the region linked to the default mode network in the same contrast. Given that excluding this result could be a Type II error, we include a brief analyses and discussion of this result in the supplementary materials (See Supplementary Figure 2).

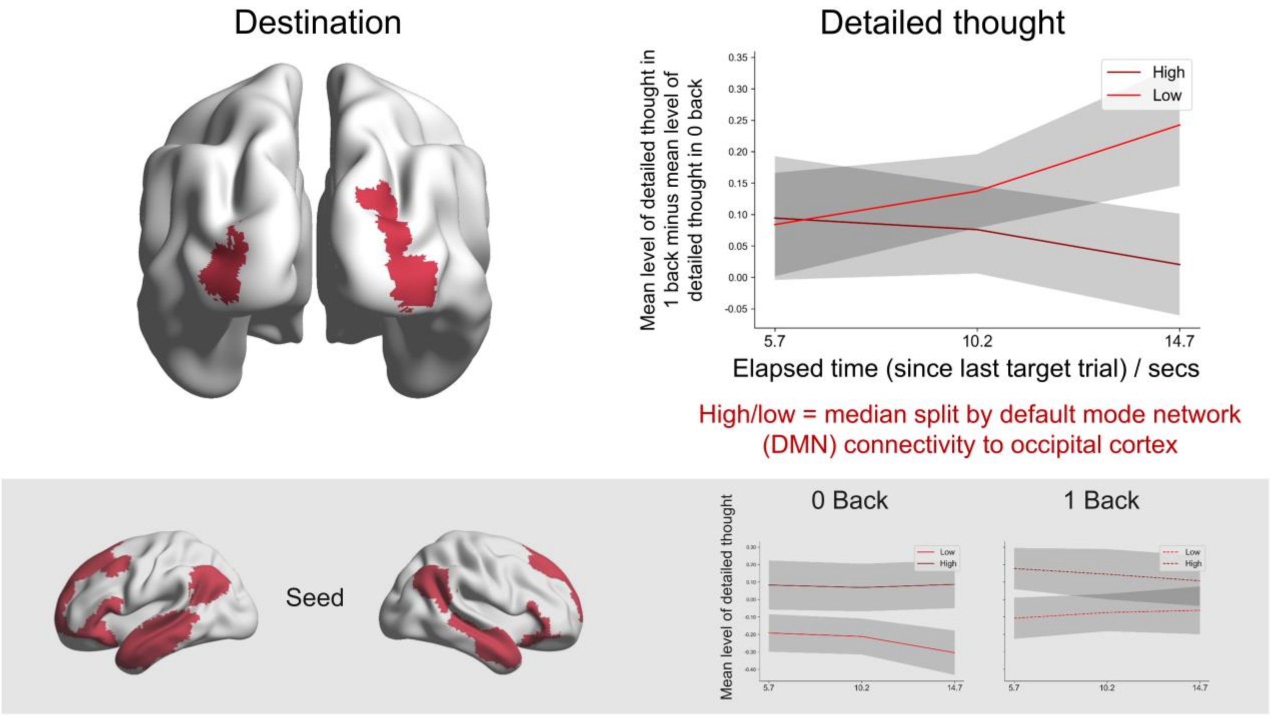

Figure 6. Group level regression using detailed PCA scores as regressors of interest revealed significant clusters for the default mode network (n=141). Connectivity between the default mode network and two significant clusters in bilateral visual cortices were related to a pattern of increasingly detailed thought in the 1-back relative to the 0-back task. Separating the group based on this connectivity revealed that the pattern of thought driving this effect was largely a decrease in detailed thought in the 0-back specifically for individuals with low, or decoupled, connectivity between these regions (bottom right). All analyses were performed using FLAME and had a cluster forming threshold of Z = 3.1 and were corrected both using FWE and to account for both the two tailed nature of our analyses and the number of models performed. The shaded areas indicate the upper and lower 95% Confidence Intervals.

Our final analysis considers the pattern of results as a collective (see Figure 7). We conducted a meta-analytic decoding of the functional associates of these effects using Neurosynth (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011). For each significant result, we decoded the terms with the strongest similarity with the spatial map generated by our analysis. These are presented in Figure 7, along with the spatial distribution of the results. In each case, our analysis revealed terms linked to perception or action. For example, “visual” was the strongest term for the default mode networks, “motor and “movement” were the strongest terms for the ventral attention network and “objects” had the greatest similarity with the dorsal attention result. Moreover, each of the four results from our study highlight patterns of coupling with regions that fall partially or completely within unimodal sensorimotor cortex as defined by Yeo and colleagues (Yeo et al., 2011). These are marked on Figure 7 by the dotted lines. These observations indicate that a broad commonality of our results is that they show coupling between attention or transmodal systems, which are thought to serve more flexible cognitive functions, with cortical regions whose functions are more directly involved in perception or action.

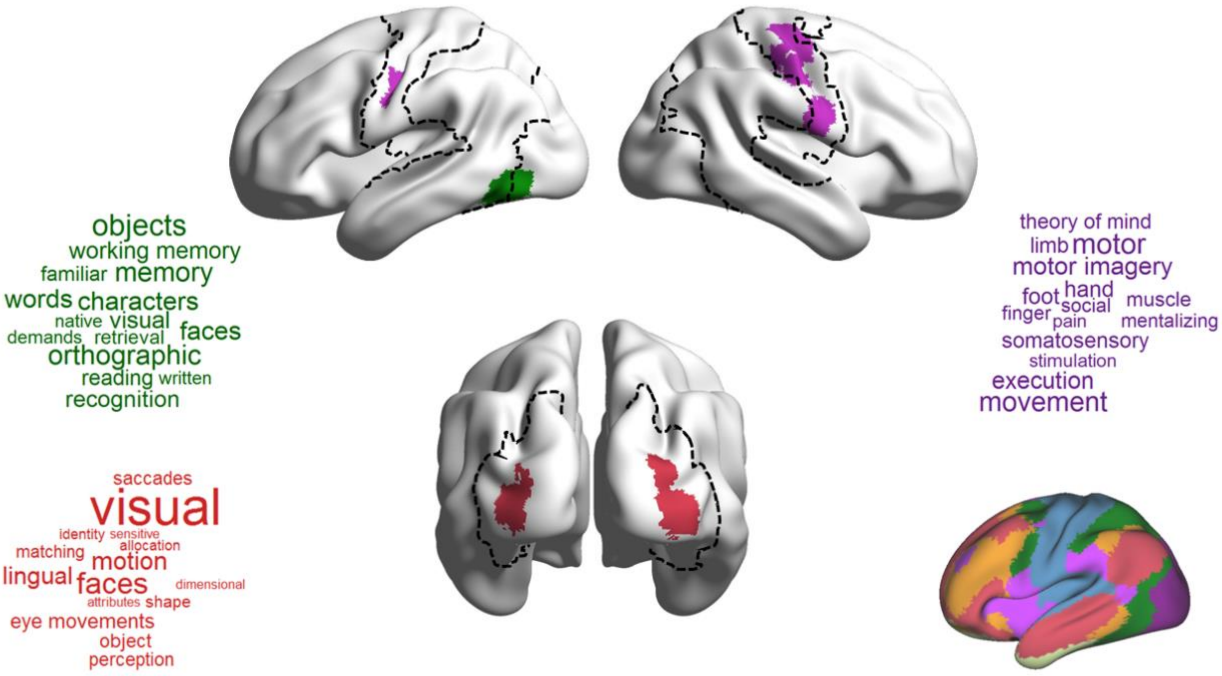

Figure 7. All significant clusters from the group level resting state analysis fall in primary sensory regions (n=141). Dotted lines show the outlines of the visual and sensorimotor networks as defined by Yeo and Krienen et al. (2011). The dorsal attention result occurred at the border of visual and dorsal attention networks. A decoding of the maps produced by this analysis using Neurosynth (Yarkoni, 2011) revealed words related to primary senses such as “motor” and “visual”, with the dorsal attention result relating to representations and semantic characteristics. The results of the decoding are displayed using word clouds where the size of the words represents the strength of the association given by Neurosynth. The Yeo networks are presented in the right hand panel to facilitate interpretation.

Discussion

Our study used a paradigm in which we time-locked patterns of thought to task events requiring an external response in both demanding and non demanding laboratory tasks. Using a between subjects design, we linked metrics that described both *transient* changes (that emerged with the passage of time between task responses) and sustained changes (that vary with the conditions of the task) to individual variation in cognitive performance and to patterns of neural organisation. Our results highlighted attention networks as dissociable by their influence on both transient and sustained dynamics of off-task thought. In addition, we found that the default mode network, levels of intrinsic coupling with regions of dorsal lateral occipital cortex were predictive of levels of detail in ongoing experience. We consider these results in terms of their implications for our understanding of the relationship between neural systems and patterns of ongoing thought.

Connectivity at rest between the ventral attention network and motor cortices was linked to greater off-task thought in the easier 0-back task and more on-task thoughts in the more difficult 1-back task. This pattern of ongoing thought is hypothesised to reflect the process of context regulation in which individuals modulate ongoing thought in line with the demands of the task (Smallwood & Andrews-Hanna, 2013). It also reflects relatively sustained changes in cognition. Altered connectivity between the motor cortices and a range of brain regions including those in the ventral attention network has been shown in individuals with ADHD (Choi, Jeong, Lee, & Go, 2013; McLeod, Langevin, Goodyear, & Dewey, 2014), a condition characterised by poorer context regulation (Franklin et al., 2017). Sustained activity in the ventral attention network is important in maintaining task sets (Dosenbach et al., 2006), the configuration of continuous data processing for a specific task, and it plays a role in encoding expected cognitive demand in order to optimise behaviour (Sheth et al., 2012). This role is supported by the correlation between this pattern of connectivity and accuracy during the performance of the tasks. It is possible that these links with motor cortex reflect the process through which appropriate cognitive and behavioural sets are maintained in the task conditions of our experiment. Consistent with this perspective, individuals showing this pattern of connectivity were more accurate at both 0 back and 1 back tasks. Based on our analysis of performance it is possible that this process describes how people regulate the context in which off-task thought occurs to minimize the likelihood that it will derail ongoing task performance.

In contrast, connectivity of the dorsal attention network with a region of lateral occipital cortex was related to an increasing degree of off-task thought when longer elapsed time intervals were compared to shorter intervals (i.e. 17 seconds versus 5 seconds). This pattern was observed in both the 0-back and 1-back tasks suggesting that it is not mediated by the task being performed. Studies suggest that the dorsal attention network is involved in the direction of attention to spatial locations (Fan, McCandliss, Fossella, Flombaum, & Posner, 2005; Hopfinger, Buonocore, & Mangun, 2000; Siegel, Donner, Oostenveld, Fries, & Engel, 2008) and to temporal intervals (Coull & Nobre, 1998). Importantly, occipital regions of visual cortex have been shown to respond transiently during sensory analysis of cues (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000) and Hopfinger et al. (2000) observed that these regions were activated simply by the presence of a stimulus. Together these data suggests that lateral occipital regions map the to-be-attended stimulus location in transient manner, while the task goal may be represented in other areas of the network (i.e. parietal regions, Corbetta et al., 2000). Consistent with this view, the correlation between lateral occipital cortex with other areas of the dorsal attention network was linked to a conscious focus on the task when behavioural relevant responses were relatively recent in time (i.e. 5 seconds) but not when the response was further in the past (i.e. 17 seconds). It is also worth noting that this connectivity was related to the same pattern of thought across both tasks, which is in line with the findings of Kuo and colleagues (2016) who showed that regions overlapping largely with this network (including the region it was correlated with in the present study) were involved in both visual and working memory search early on in processing. Interestingly, in our data this pattern of coupling was linked to greater creativity and intelligence. Associations with fluid intelligence suggests that this pattern does not reflect problems in attentional control and so is not an example of executive failure (McVay & Kane, 2010). Studies have shown that off-task thought attenuates selective attention (Smallwood et al., 2008) and performance monitoring (Kam et al., 2012), while set-shifting is maintained (Kam & Handy, 2014). Our result might point to individual differences in these population-level effects (Handy & Kam, 2015), with more creative and intelligent individuals displaying a more dynamic and flexible recruitment of these resources. Based on our behavioural analysis we suspect that intelligent individuals may exploit the transient task focus supported by coupling the dorsal attention network to lateral occipital regions focus on task relevant information when changes in the external environment dictate that this may be important.

Unlike the attention networks, which were linked to patterns of off-task thought, analysis of the default mode network indicated that its coupling with regions of lateral occipital cortex were linked to reports of experiences with vivid detail. In particular, individuals with higher coupling had greater levels of detail. Individuals with lower levels of coupling was linked to decreasing levels of detail as elapsed time increases in the less demanding 0-back task. This pattern of results may reflect the possibility that patterns of intrinsic connectivity between the default mode network and visual regions are important for experiences with greater clarity and detail. It is unclear whether this pattern reflects details that are relevant to the task or not. While initial views of the default mode network assumed that it was a task-negative system, this view is increasingly coming under scrutiny (Spreng, 2012). Critical to the current study, the default mode network plays a role in 1-back decisions in this paradigm (Konishi et al., 2015; Murphy et al., 2018) while other studies suggest that it may be important when an individual is “in the zone” (Esterman, Rosenberg, & Noonan, 2014; Kucyi, Hove, Esterman, Hutchison, & Valera, 2016). Moreover, studies that probe the subjective aspects of memory (such as its vividness) suggest that it can be determined from neural patterns within the posterior cingulate (Richter, Cooper, Bays, & Simons, 2016), while the application of TMS to regions of angular gyrus disrupt the retrieval of specific conceptual knowledge (Davey et al., 2015). These studies together provide a precedent for the view that that the default mode network may not simply be a task negative system but can be important in maintaining task relevant details. Future studies may wish to explore the possibility that the default mode network is important for aspects of experience related to the task, as well as simply for elements that are unrelated to the task being performed.

Our behavioural analysis suggests that decreased detail in longer intervals was related to better inhibition of previously relevant information (Whitmer & Banich, 2007). It is possible, therefore, that one explanation for why patterns of default mode to visual network coupling are linked to experiences of vivid detail is because co-activation of these regions with transmodal cortex enables regions of the default mode network to help support detailed representations of task relevant information, especially when the task involves updating of information in memory based on external input. Our study suggests that while coupling between the DMN and visual cortex reflect higher detail across both task contexts, in the easier 0-back task, the passage of time was linked to reductions in detailed thought in individuals in which these regions were decoupled at rest. Cognition in the 0-back task, does not rely on continual perceptual coupling (Kang, Huffer, & Wheatley, 2014; Smallwood et al., 2011) and it has been argued that the absence of a requirement for perceptual coupling is a condition that allows cognition to focus on representations that are not present in the external environment (Smallwood, 2013). We speculate that the reductions in detail that emerge with the passage of time in the 0 back task may reflect the decoupling of the default mode network from information relevant to the task, allowing attention the opportunity to focus on self-generated information.

Finally, our study highlights the importance of temporal dynamics when considering the processes that contribute to patterns of ongoing cognition (Smallwood, 2013). Our data suggests that in contexts in which external behaviour is only intermittent, the amount of elapsed time since the last moment of interaction with the external environment provides meaningful information on the ongoing cognitive state. Notably our results highlight that this process may depend on the interaction between regions of attention or transmodal cortex and more specialised unimodal cortex, such as those important for vision or sensorimotor function. Our prior work highlighted that different large-scale networks can be organised on a dimension that spans unimodal to transmodal cortex (Margulies et al., 2016), suggesting a spatial gradient linked to increasingly stimulus-independent processes. Viewed from this perspective, it is intriguing that patterns of temporal changes in whether the task is experienced with vivid detail, or is related to the task, depends on correlated brain activity between higher-order brain systems and those that are generally anchored in unimodal regions that support perception and action related to the here and now.

There are several limitations associated with our study methodology we that should be borne in mind when considering the implications of our results. First and foremost, we used a between subject analysis to examine the emergence of temporal dynamics and so does not describe the momentary changes in neural function that vary with changes in cognition. Instead, our individual difference analysis captures the association between how cognition changes in the laboratory and variations in both cognitive and neural processing. Both psychology and neuroscience have a venerable tradition of understanding cognitive processes by exploiting patterns of trait variation. In neuroscience, for example, this approach has been used to understand neural traits that support a wide range of forms of cognition as measured in the laboratory including intelligence, well-being, and meta cognition (Baird et al., 2013; Finn et al., 2015; Smith et al., 2015). An individual variation perspective has also been informative in studies of ongoing thought (Golchert et al., 2017; Kane et al., 2007; McVay & Kane, 2012; Smallwood et al., 2016). One advantage of the between subject approach is that it affords the possibility of achieving larger sample sizes that are likely to provide better estimates of the real effect, an issue that has recently become important in both psychology and neuroscience (Yarkoni, 2009). It also allows measurement of neural processing in the absence of the interruptions that are caused by experience sampling (Konishi & Smallwood, 2016) allowing neural processes to be described in a straightforward manner. The validity of this approach, however, rests on the stability of the measures of experience and neural processing upon which our analysis depends. Our study measured ongoing experience in the laboratory across three separate days providing a stable measure that cannot be attributed to fluctuations at a very short time frame (e.g. over 24 hours). Moreover, while we only assessed neural function once, recent intensive studies of neural organisation of single participants suggest that patterns of functional connectivity are both stable across time and relatively specific to individuals (Gratton et al., 2018). Finally, the patterns of dynamics at rest upon which this study depends are both consistent across different sessions and are stable across siblings, suggesting that they are in part heritable (Vidaurre, Smith, & Woolrich, 2017). Together these lines of evidence provide confidence that our data reflects relatively stable features of an individual, suggesting that we are likely to have captured patterns of population variation in relationships between ongoing thought and variation in neuro-cognitive function. Nonetheless, the most robust evidence for the neural traits that support different patterns of ongoing thought would be provided by a design that measured both neural function and ongoing thought in the same individuals at multiple time points as this design would allow state and trait differences in processing to be characterised within the same design. We recommend that future work explores this possibility.

A second issue is whether the patterns of association between ongoing thought and neural and cognitive processing observed in our study reflect associations between the patterns of thoughts a participant experiences across different situations, or whether they reflect the neurocognitive architecture that pre-disposes individuals to particular experiences within the laboratory. We know from studies linking patterns of ongoing thought to behavioural measures, that individuals who tend to perform poorly on measures of attentional control do so in part because they fail to refrain from off task thoughts in tasks that measure attentional control (Mrazek et al., 2012). Importantly, this issue is not likely to be specific to studies seeking to explain patterns of ongoing thought. For example, associations between intelligence and intrinsic organisation may emerge because intelligent people have specific patterns of experience at rest (Finn et al., 2015). Likewise, associations between intrinsic neural organisation and meta cognition (Baird et al., 2013) may arise because individuals who are good at meta cognition tend to frequently take stock of the contents of their experiences, a process known as meta awareness (Schooler, 2002). Recent work in our group has provided some evidence for this latter perspective. Using canonical correlation analysis, Wang and colleagues (2018) decomposed patterns of neural activity at rest with a series of self-reported items administered at the end of the scan and that described the individuals experience during this period. We identified a pattern of cognition that was characterised by reduced correlation within the attention networks and that was linked to patterns of thinking focused on an individuals current concerns. This component was linked to worse performance on a battery of cognitive tasks measuring general levels of aptitude. This data not only supports the current analysis highlighting that task focus is linked to the intrinsic architecture of the attention networks, it also suggests that particular patterns of cognition at rest may be important mediators in links between neural activity and laboratory task performance. While resolving why intrinsic neural activity predicts measure of laboratory cognition is clearly beyond the scope of this investigation it is nonetheless an important question for future research. For example, future studies using in-scanner methods should enable more robust classification of the dynamic patterns of brain activity that occur during attentional switches and that help maintain external trains of thought.

Finally, it is also important to note that the task paradigm we used likely reflects an important boundary condition. While the consistent relationship between measures of ongoing cognition, cognitive performance, and patterns of neural activity at rest, provide confidence in the validity of our results, aspects of these patterns are likely to be specific to certain aspects of our experimental design. For example, the stimuli in our experiment were shapes and so had only minimal semantic content. It seems likely that in environments containing stimuli with richer semantic or episodic associations, the dynamics of ongoing cognition and their associated neural processes would be different. For example, in a prior study presenting stimuli with meaningful associations in a broadly similar task context increased activity in many regions of the default mode network (Murphy et al., 2018). Given the important contextual boundaries for understanding influences on ongoing thought (Smallwood & Andrews-Hanna, 2013) it is possible that the dynamics between this network and states of vivid detail could vary in a task dependent way that is enhanced when the nature of stimulus input can be more readily incorporated with internal representations. Our study also used visual information and it is possible that this aspect of our design explains why many of our results highlight regions of occipital cortex.

Conclusions

In conclusion, our study reveals a novel pattern of temporal dynamics that can be related to changes in ongoing cognition that have their roots in both cognitive traits, such as creativity and intelligence, and in the intrinsic architecture of the cortex. We identified that neural systems involved in attentional process are important influences in constraining the dynamics of off-task thought, with the dorsal system important for transient changes, and the ventral system for more sustained changes. These data provide evidence in support for the view that off task cognition is not necessarily synonymous with the default mode network, but instead may be related to activity within the attention systems. We also identified that at least some of the processes that mediate patterns of ongoing thought are context specific, with our analysis suggesting that the ventral attention network is important for regulating patterns of task focus in a manner that is consistent with the demands imposed by the ongoing task. Future studies should attempt to identify the dynamic interactions of these networks during in-scanner task performance, as well as to further clarify the links seen between intrinsic patterns of connectivity, patterns of thought, and cognitive phenotypes.

Supplementary material

Figure S1. Scree plot

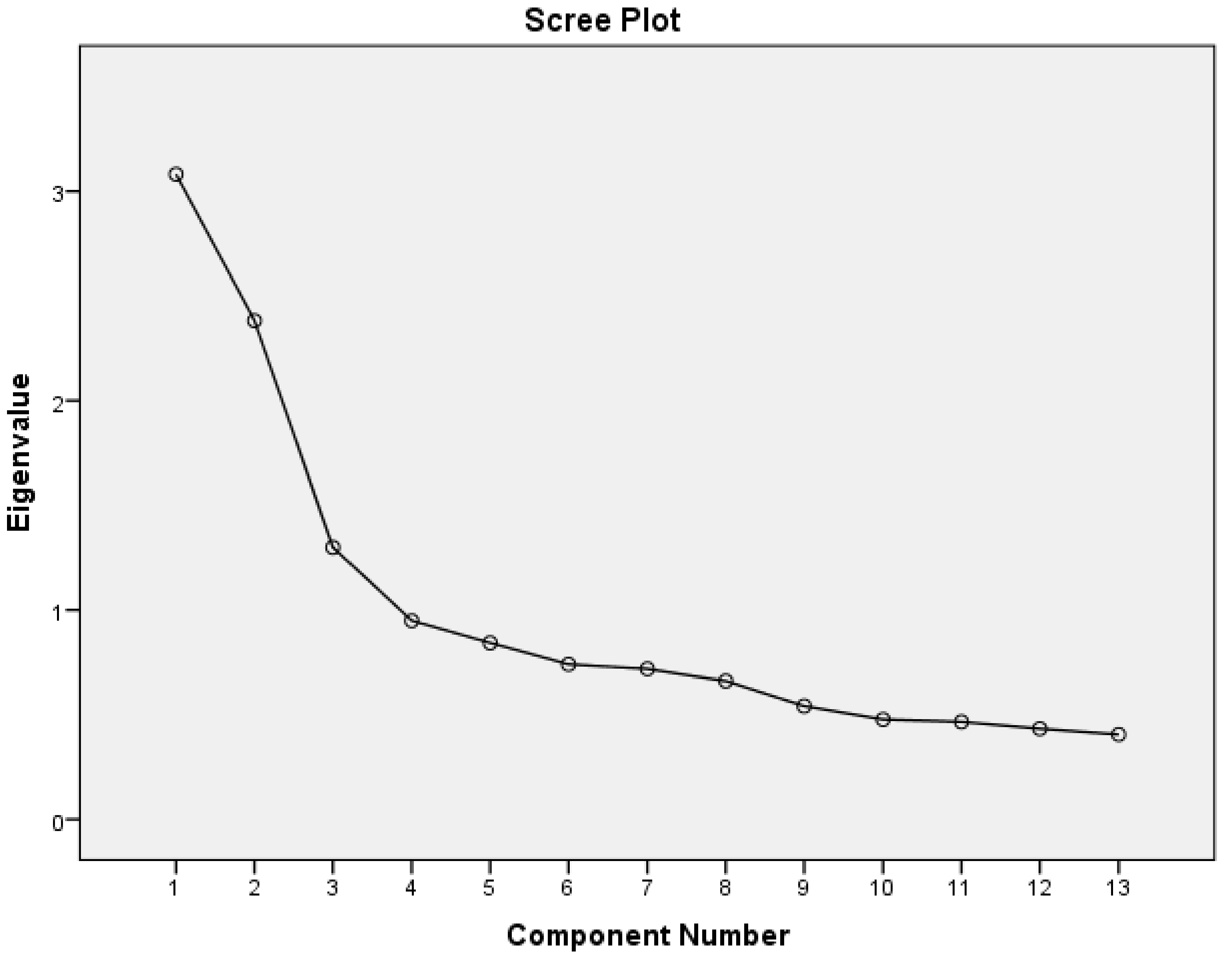

Figure S 1: Scree plot from PCA used to select number of components (4)

Component	Total Eigenvalue	% Variance explained	% Cumulative variance
1: Detail	3.081	23.703	23.703
2: Off-task	2.383	18.329	42.032
3: Modality	1.299	9.995	52.027
4: Emotion	0.948	7.295	59.322

Table S 1: Eigenvalues for the 4 components of thought

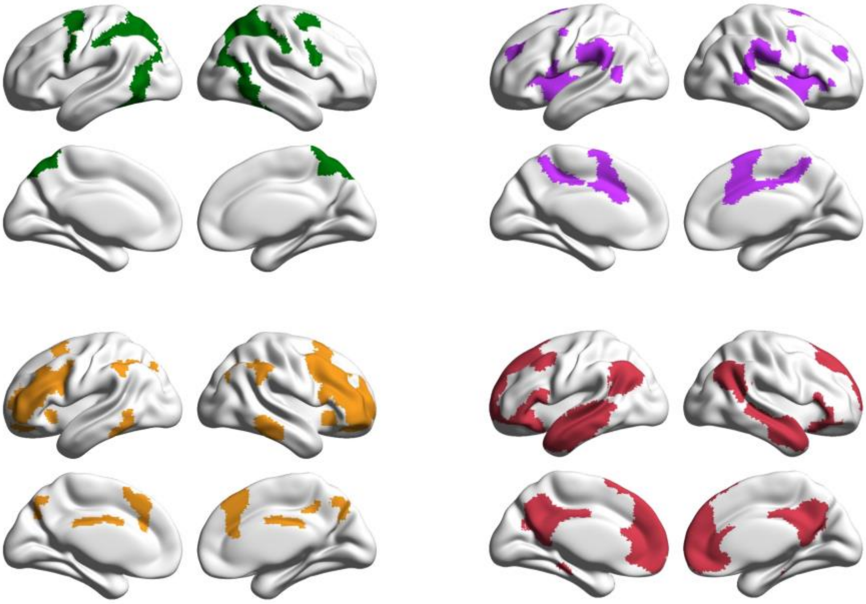

Figure S 2. Seeds for the (from top left clockwise) dorsal attention, ventral attention, default mode, and frontoparietal networks from Yeo and Krienen et al., (2011).

Seed	Thought component	Contrast	Cluster size	MNI coordinates	Significance
DAN	Detail	Linear decrease	243	(16, 18, -10)	p=.00898
	Off-task	**Linear increase**	**321**	**(-46, -62, -12)**	**p=.00206**
	Off-task	Linear decrease	230	(2, -8, 44)	p=.0116
VAN	Detail	0back > 1back	174	(12, -54, 34)	p=.0361
	Off-task	**0back > 1back**	**901**	**(50, -18, 42)**	**p=2.98e^{-7}**
			521	**(-46, -14, 26)**	**p=6.71e^{-5}**
FPCN	Detail	Time by task (0back increase, 1back decrease)	249	(44, -90, 0)	p=.00699*
DMN	Detail	0back > 1back	245	(42, -88, 4)	p=.00944
	Detail	**Time by task (0back increase, 1back decrease)**	**687**	**(36, -92, -2)**	**p=7.93e^{-6}**
			297	**(-34, -92, 2)**	**p=.00355**

Table S 2. All significant clusters at p<.05 (two-taled), Z>3.1 FWE-corrected. Clusters in bold are the main results discussed in the paper that passed Bonferroni correction for multiple comparisons (p<.0625). * denotes trending result (see below).

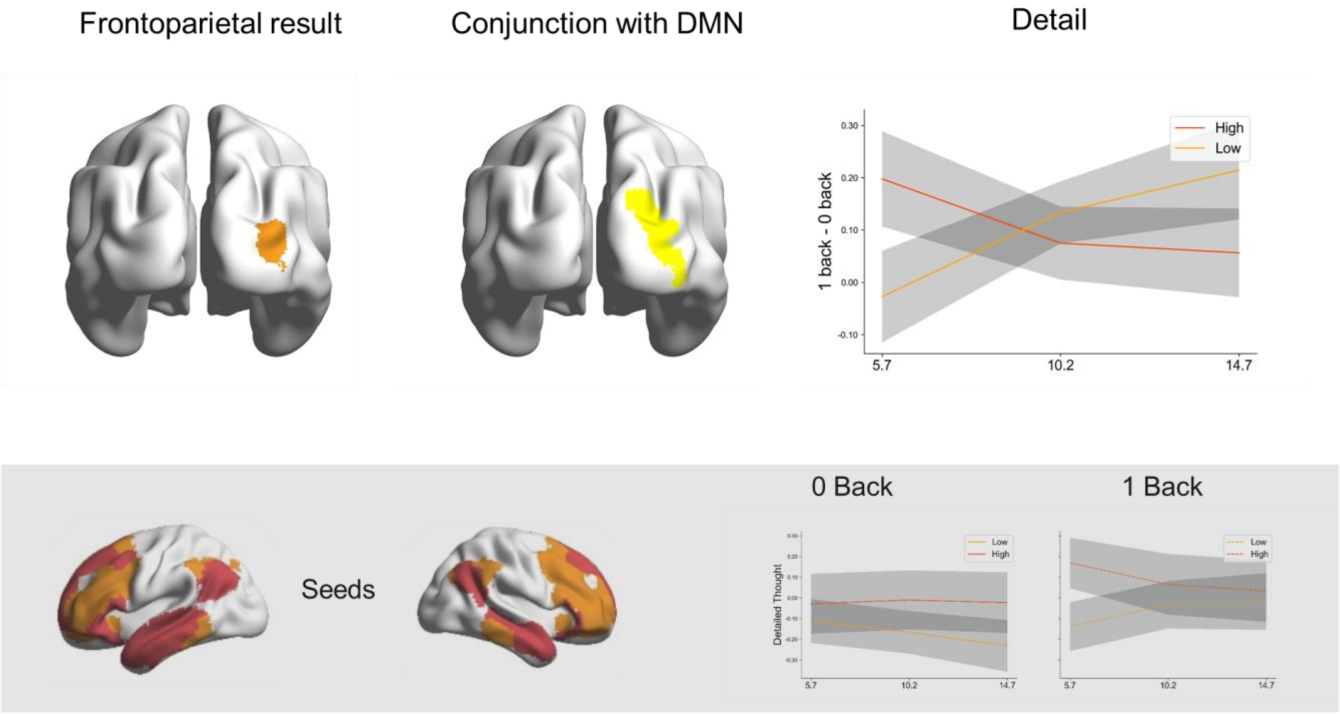

Figure S 3. Trend level fronto parietal network effects. Splitting the participants based on their patterns of connectivity revealed that strong connectivity was associated with greater detail in the 1-back task at earlier intervals while lower levels of connectivity was linked to patterns of increasing detail in the later intervals. The fronto-parietal and default mode network effects involved overlapping regions of visual cortex. We confirmed the significance using formal whole brain conjunction that revealed a significant overlap with the prior default mode network at Z = 2.6 (see middle right hand panel, no results were significant at Z = 3.1). Higher coupling between the frontoparietal network and visual cortex was related to more detailed thought immediately following a task event in the 1-back task. Interestingly, this is an opposing effect to that seen in the default mode network (decoupling related to decreased detail at late time points in the 0-back task). This may relate to the roles of these networks in managing cognitively demanding information (Klingsberg et al., 1997) and “in the zone” states (Esterman et al., 2016), respectively.

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