States of Mind: Understanding Ongoing Thought using Functional Magnetic Resonance Imaging

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Doctor of Philosophy

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Cognitive Neuroscience and Neuroimaging

April 2020

Abstract

Ongoing thought makes up a large portion of daily life, and has been associated with varied neurocognitive processes and outcomes, including poor task performance and creativity, negative mood and improved well-being. This complexity arises due to the fact that (1) ongoing thought is multi-dimensional in nature (2) the context during which thought occurs has an important impact on its outcomes and (3) moments of stable, maintained cognition differ conceptually from transitions between states. These issues have led to disagreements in the literature about the role of certain systems during ongoing thought, particularly executive control and the default mode network. This thesis used a paradigm that measures ongoing thought using multi-dimensional experience sampling to capture state contents across two tasks that vary in their need for continuous monitoring. By placing ongoing thought within a multi-dimensional state space, including time and context as independent variables, and using fMRI as a covert measure of state and trait processing, this paradigm enabled a clearer delineation of the neurocognitive systems engaged during ongoing thought. Results point to a role for the ventral attention network in monitoring external context to guide general state maintenance and a role for the dorsal attention network in transitioning between internal and external states. The default mode network was related to detailed thoughts and shown to be important for determining state contents through its interaction with perceptual regions. Executive resources were engaged to maintain both internal and external states, and fluid intelligence was associated with the ability to transition between these states in the most effective manner in line with the demands of the environment. Finally, state transitions were shown to involve whole-brain reorganisations along multiple dimensions that are rooted in the functional organisation of the brain at rest.

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Acknowledgements

I am thankful to my supervisor, Dr. Jonny Smallwood, for his theoretical, practical, and motivational insights, both in the production of this thesis and during my 3 years working with him. His mentorship has helped me navigate a challenging period in terms of both work and life more generally. I feel I have grown significantly as a researcher, and I am deeply grateful for his support. I am also grateful to Dr. Tammy Vanderwal for helping me to secure this amazing position.

I am also thankful for the support of various lab mates who have come and gone during these 3 years, and have provided essential practical and theoretical contributions to this project: Hao-Ting Wang, Charlotte Murphy, Theo Karapanagiotidis, Deniz Vatansever, Mladen Sormaz, and Nerissa Ho. I am also grateful for the friendship of Bronte McKeown and Delali Konu who have been motivating office mates during my final year, and who I am sure will add to the findings in this thesis in unique and important ways.

Daniel Margulies, Boris Bernhardt, Elizabeth Jefferies, Hugo Critchley and Sarah Garfinkel, and Robert Leech have also been wonderful collaborators to have, and I am grateful for all of the time spent talking about research, in universities and pubs around the world.

Finally, I am thankful to my parents, and my fiancée Carson Kautz for their emotional support. I couldn't have made it through without them.

Author's Declaration

I, Adam Turnbull, declare that this thesis is a presentation of original work and I am the sole author, under the supervision of Dr. Jonny Smallwood. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

The empirical work presented in this thesis has been published in the following peer-reviewed journals:

Turnbull, A., Wang, H. T., Schooler, J. W., Jefferies, E., Margulies, D. S., & Smallwood, J. (2019). The ebb and flow of attention: Between-subject variation in intrinsic connectivity and cognition associated with the dynamics of ongoing experience. *NeuroImage*, *185*, 286-299.

Turnbull, A., Wang, H. T., Murphy, C., Ho, N. S. P., Wang, X., Sormaz, M., ... & Smallwood, J. (2019). Left dorsolateral prefrontal cortex supports context-dependent prioritisation of off-task thought. *Nature communications*, *10*(1), 1-10.

Turnbull, A., Garfinkel, N., Ho, N., Critchley, H. D., Bernhardt, B., Jefferies, E., & Smallwood, J. (2020). Word up – experiential and neurocognitive evidence for associations between autistic symptomology and a preference for thinking in the form of words. *Cortex* (in press).

Turnbull, A., Karapanagiotidis, T., Wang, H. T., Bernhardt, B., Leech, R., Margulies, D., Schooler, J., Jefferies, E., & Smallwood, J. (2020). Reductions in task positive neural systems occur with the passage of time and are associated with changes in ongoing thought. *Scientific Reports* (in press).

Chapter 1 – Introduction and Review of Literature

1.1 Introduction

Ongoing thought is dynamic, as characterised by William James' classic metaphor of a stream (James, 1890). Within this stream, there are "perches" where the mind is focused on one train of thought or external task, and "flights" where the mind moves between these states. While much research has been done trying to understand how individuals switch focus between external tasks (Monsell, 2003), it is less well established how we switch between external and internal mental states. These internal mental states, such as mind wandering, have recently become the focus of much research in cognitive neuroscience (Smallwood & Schooler, 2015), in part driven by the expansion of functional magnetic resonance imaging (fMRI) as a means to understand the covert mechanisms underlying internal experience. Two main themes have come out of this research: that ongoing experience is heterogeneous, and that it is very important what we think about and when we do it.

This introductory chapter will review a range of studies that have used various techniques to understand the contents of thoughts. Predominantly, these are focused around the use of "experience sampling", a method by which participants are asked questions about their thoughts in various contexts. It will describe what this technique has taught us about the contents and outcomes of ongoing thought and how these vary across the population, as well as summarising the neural underpinnings of the processes involved in ongoing thought that have so far been identified using fMRI. In doing so, it will:

- highlight the importance of viewing ongoing thought as heterogeneous in nature, containing multiple dimensions with varied neural underpinnings and outcomes
- highlight the need to take into account context when attempting to understand the outcomes and neurocognitive systems associated with ongoing thought

It will then suggest that ongoing thought can be understood as the movement of the mind through multi-dimensional state space, within which states are either maintained or transitioned between. Using this framework, it will go on to:

- elaborate what we know about the neurocognitive systems that are engaged while states are maintained, with particular attention being payed to contentious

issues in the literature, such as the role of the DMN and executive control in internal state maintenance

- describe difficulties researching state transitions, before showing how novel dynamic approaches to analysing fMRI data are being used to overcome these challenges

Finally, it will use this literature review to provide the motivation behind the paradigm used in this thesis and allow the findings of the later chapters to be embedded within a wider context

1.2 The Contents of Ongoing Thought

The content of ongoing thought can conceivably vary from mundane daily plans to the furthest reaches of human imagination. While this makes its study difficult, research has shown that there are common themes and structure to what we think about. For example, people spend more time thinking about the future than the past (Baird, Smallwood, & Schooler, 2011; Iijima & Tanno, 2012; Ruby, Smallwood, Engen, & Singer, 2013; Smallwood et al., 2011; Smallwood, Nind, & O'Connor, 2009; Song & Wang, 2012; Stawarczyk, Majerus, Maj, Van der Linden, & D'Argembeau, 2011), and they largely consider things of personal relevance to themselves (Stawarczyk, Cassol, & D'Argembeau, 2013). An array of methods has been used to extract information about what an individual is thinking about. Generally, these begin by asking the person a range of questions about the contents of their thoughts. This occurs either retrospectively, with a questionnaire at the end of an experimental period (Barron, Riby, Greer, & Smallwood, 2011; Gorgolewski et al., 2014; Smallwood, Brown, Baird, Mrazek, et al., 2012), or using probes that occur randomly (probe-caught (M. S. Franklin, Smallwood, & Schooler, 2011; Smallwood & Schooler, 2006)) or when an individual indicates that they have entered an experimenter-defined state (self-caught (M. S. Franklin, Broadway, Mrazek, Smallwood, & Schooler, 2013)). Using multiple questions instead of one simple response (e.g. "were your thoughts on- or off-task?") is known as multi-dimensional experience sampling (MDES) and allows a more thorough investigation into the contents of ongoing thought. The work in this thesis will use MDES during task performance in a probe-caught paradigm.

Once multi-dimensional experience sampling data has been collected, researchers often use data-driven methods, such as principal component analysis

(PCA), to identify patterns. One of the benefits to using dimensionality reduction techniques like PCA is that they look for patterns in the data to separate out components that capture unique and meaningful variance. This enables researchers to describe specific types of thought in a data-driven manner, and avoids the need to define abstract concepts prior to data collection. There has been much debate, for example, on what defines certain types of thoughts, such as "mind wandering". To some, it is an issue of intentionality (Seli, Risko, & Smilek, 2016b) and for others an issue of constraints (Christoff, Irving, Fox, Spreng, & Andrews-Hanna, 2016) or dynamic properties (Mills, Raffaelli, Irving, Stan, & Christoff, 2018). These are important theoretical debates, and much progress has been made on moving toward a consensus on definitions in the field (Seli, Kane, et al., 2018), but these arguments can be difficult to solve empirically. Viewing ongoing thought in terms of states with specific contents that can be characterised empirically means that they do not need to be specifically defined in order to utilise these methods to improve our understanding of the neurocognitive systems involved. For the purposes of this thesis the term 'ongoing thought' will be used to describe the heterogeneous experience that is characterised with MDES. 'Mind wandering' will be used in some cases to describe previous research that used the term to mean certain types of ongoing thought that are task-unrelated in nature, but it should be noted that the exact definition of this term may vary between studies.

1.2.1 Dimensions of Thought

Studies using dimensionality reduction approaches to study MDES data have identified replicable components that consistently explain large amounts of the variance in ongoing thought content. For example, studies using PCA have shown that thoughts vary along four key axes: task-relatedness, level of detail, modality (images or words), and emotional valence (Konishi, Brown, Battaglini, & Smallwood, 2017; Poerio et al., 2017; Ruby, Smallwood, Engen, et al., 2013). Similar methods, such as hierarchical clustering, also found emotional valence as a dimension, as well as whether the thoughts were past or future related (Andrews-Hanna et al., 2013). This was replicated by Gorgolewski and colleagues (2014) who found all of the factors from the previous two studies, as well as one describing thoughts about other people (social cognition). The components in this study were shown to vary by age and have distinct neural correlates. Two further studies used sparse canonical correlation analysis

(CCA), a cousin of PCA that looks for shared components in two groups of variables to find components of thought and associated neural correlates. The first identified two dimensions of thought with associated neural connectivity: positive-habitual experiences and spontaneous off-task thoughts (H.-T. Wang, G. Poerio, et al., 2018). The second looked at whole brain patterns of connectivity and retrospective measures of thought and found three separate components of thought: 'purposeful', 'emotional', and 'personally important', each with a different whole-brain pattern of related connections (H.-T. Wang, D. Bzdok, et al., 2018). These studies highlight that ongoing thought is heterogeneous in nature, with thoughts existing along multiple dimensions with dissociable neural correlates.

1.2.2 Neural Correlates of Ongoing Thought

The main problem with using MDES as the only measure of experience is that, depending on the questions asked and decomposition techniques used, it can lead to varying answers to the structure of thought without a means of assessing whether these are meaningful. For example, while studies using PCA and hierarchical clustering find components that share elements, there are differences in how they group together: one approach may find that social aspects of thought form a component of "off-task" experience along with memory processes (Konishi et al., 2017; Poerio et al., 2017; Ruby, Smallwood, Engen, et al., 2013), while others may separate these into distinct factors (Gorgolewski et al., 2014). While it is not necessary for either answer to reflect the "true" nature of thought for them to have empirical value, it is vital that studies using different experience sampling questions and decomposition methods are comparable for the field to progress. Comparing these components to other measures of cognition is therefore not only useful mechanistically, it is essential to validate that these measures are capturing meaningful information about ongoing thought. If multiple studies identify similar cognitive or neural systems as involved in the same types of ongoing thought, it not only suggests that these systems play a role in these thoughts, but provides further validity to the methods. If these systems are consistently identified in non-experience sampling research in relation to cognition that is included along that same dimensions of thought, that would give further confidence in the findings. Take as an example that the default mode network (DMN) has been shown to be involved in memory-guided processing during task performance (Konishi, McLaren, Engen, & Smallwood, 2015; C. Murphy et al., 2018; C. Murphy, Wang, et

al., 2019; R Nathan Spreng & Grady, 2010). Studies using different approaches to measuring ongoing thought using MDES have captured components of thought that involve memory-related processes and relate to processing in the DMN (Poerio et al., 2017; Smallwood et al., 2016; H.-T. Wang, D. Bzdok, et al., 2018). This suggests that the DMN is performing processing that is shared between memory-guided task performance and specific memory-related dimensions of ongoing thought, and gives confidence that these studies are capturing meaningful information about ongoing thought using MDES.

As a technique that provides researchers with a measure of real-time cognitive processing, fMRI is intrinsically suited to enable a more thorough investigation of ongoing thought processes. Indeed, the rise in the popularity of fMRI as an experimental tool is partly responsible for the concurrent expansion in research into internal thought (Callard, Smallwood, Golchert, & Margulies, 2013). There are two main approaches to studying ongoing thought using fMRI. The first measures brain activity simultaneously with experience sampling (Christoff, Gordon, Smallwood, Smith, & Schooler, 2009; Sormaz et al., 2018) or during periods when specific types of thought are likely to be engaged (Ellamil et al., 2016; Hasenkamp, Wilson-Mendenhall, Duncan, & Barsalou, 2012; Konishi et al., 2015). This means that brain activity can be linked directly to certain states in-the-moment or across blocks. The second approach leverages the fact that ongoing thought shows consistent patterns within a person suggesting it has trait-like elements (Seli, Risko, & Smilek, 2016a). Brain activity measured at rest gives insight into the trait architecture of the brain that represents a person's unique identity (Finn et al., 2015) that includes these trait-like ways of thinking. This brain activity can therefore be related to measures of ongoing thought collected either during the same resting period, or during a subsequent task to gain knowledge about the neural systems underlying certain aspects of experience (Martinon, Smallwood, McGann, Hamilton, & Riby, 2019). This section will review studies from task-based and resting state fMRI to introduce these techniques and show that ongoing thought relates to multiple large-scale brain systems that include, but are not limited to, the DMN. It will also highlight the additional insights that have been gained by considering ongoing thought as multi-dimensional in nature.

1.2.2.1 Task-based fMRI

An early and still widely used analysis method for fMRI data is to compare two periods of time that differ in their demands to assess which brain regions are more active during, and therefore likely related to, which processes (often referred to as task-based fMRI). Early studies using this technique identified the DMN by its task-related decreases in activation (Greicius, Krasnow, Reiss, & Menon, 2003; Raichle et al., 2001; Shulman et al., 1997) and subsequently linked this network to mind wandering (Mason et al., 2007). A study looking at the period just before a subjective report of off-task thought (compared to the same period preceding an on-task report) found that regions in both the DMN and frontoparietal control network (FPCN) were more active (Christoff et al., 2009). These analyses were limited by their comparison of a very specific type of task processing to a poorly defined and heterogeneous off-task state. More recent studies now suggest that the DMN is far from being exclusively an off-task network (R Nathan Spreng, 2012). For example, it has been shown to activate during large shifts in cognitive sets (Crittenden, Mitchell, & Duncan, 2015), particularly those that require cognition to be guided by information that is unrelated to perceptual input (Konishi et al., 2015; C. Murphy et al., 2018; C. Murphy, Wang, et al., 2019; Smallwood, Tipper, et al., 2013). One reason it may be perfectly placed to enable internal cognition is that it lies at the opposite end of a neural gradient, which is anchored at the other end by sensory regions, both in terms of geodesic distance and the intrinsic functional organisation of the cortex (Margulies et al., 2016). This position at the extreme of a functional hierarchy makes it able to process and integrate transmodal information (Mesulam, 1998), as well as providing it with protective layers of cognitive processes through which sensory information has to travel before it can interrupt its function.

Researchers have also used repetitive tasks to maximise off-task thoughts, while utilising the fact that off-task periods are related to performance errors (McVay & Kane, 2012b) to model the brain in these states. One such study found that part of the DMN was related to both task-unrelated thoughts and response inhibition, but that the latter process also engaged additional regions, suggesting both shared and segregated processing (Allen et al., 2013). Error-awareness was related to DMN and ventral attention network (VAN) recruitment. Stawarczyk and colleagues differentiated thought reports during task performance based on whether they were related to the

task and related to perceptual input (Stawarczyk, Majerus, Maquet, & D'Argembeau, 2011). They found that while some regions of the DMN were active during both task-unrelated and perception-independent thought, others were only active during perception-independent thought, suggesting a role for the DMN in supporting task states with relevant but internally-guided cognition. These studies highlight the fact that the DMN seems necessary for internal experience but does not appear to be specific to these states.

1.2.2.2 Resting State fMRI

Resting state fMRI measures brain activity while the participant is in an unconstrained state. There are two related approaches to using resting state fMRI to understand ongoing thought. The first is based on the idea that the patterns of brain activity during the resting state are related to the thoughts that occur over that period. Therefore, by combining resting state fMRI with a measure of experience taken at the end of this resting period researchers can gain insight into these processes. One study using this approach showed that "purposeful" thought was related to reduced connectivity between a range of large-scale brain networks including the DMN and attention networks (H.-T. Wang, D. Bzdok, et al., 2018). It also identified three other significant components of thought with associated neural connectivity that involved whole-brain, multiple-network changes. Similarly, another study using a similar approach identified a wide range of brain regions whose connectivity was significantly related to different aspects of ongoing thought (Gorgolewski et al., 2014).

Another approach to understanding the links between ongoing thought and brain connectivity is to use measures of ongoing thought from a separate period of time. This takes advantage of the fact that ongoing thought has trait-like aspects that are consistent across time within an individual (Seli et al., 2016a). The first of these studies found that connections from separate seeds within the temporal lobe that were related to two different dimensions of thought overlapped in the posterior cingulate cortex (PCC) (Smallwood et al., 2016). This region is a hub within the DMN, suggesting that this network is important in integrating information to provide complex, rich internal experiences (Villena-Gonzalez et al., 2018). A second study found that integration between the DMN and FPCN was related specifically to intentional but not spontaneous "mind wandering", highlighting the flexible recruitment of component

processes in a manner that reflects the nature of the experience (Golchert et al., 2017). Similarly, having strong connections within the DMN was related to poor external engagement as well as off-task future thoughts, two states that engage the shared process of perceptual decoupling and internally-guided cognition (Poerio et al., 2017). Another study found that different components of thought had associated connectivity patterns within the DMN that related in a dissociable manner to executive control and the ability to generate information (H.-T. Wang, G. Poerio, et al., 2018). Taken together, these findings support the involvement of the DMN, along with other large-scale brain networks, in ongoing thought. Additionally, they highlight the heterogeneous nature of experience and the important knowledge that can be gained by measuring multiple aspects of ongoing thought using MDES. Finally, the consistent identification of overlapping neural systems provides validation that the measures obtained using MDES are capturing meaningful, reliable dimensions of experience.

Overall, research using MDES to understand ongoing thought has found that ongoing thought is heterogeneous in nature but contains meaningful patterns that can be reliably identified using dimensionality reduction techniques such as PCA (Konishi et al., 2017; Poerio et al., 2017; Ruby, Smallwood, Engen, et al., 2013; Sormaz et al., 2018). This approach to understanding ongoing thought using MDES avoids abstract arguments about precise definitions of certain types of thought (Seli, Kane, et al., 2018), but can make interpreting, consolidating, and having confidence in disparate findings challenging. Using fMRI as an objective measure of experience can help validate MDES approaches, as the consistent identification of brain networks relating to specific aspects of ongoing thought across studies suggests meaningful information is being obtained. Studies using fMRI and MDES have shown that, rather than involving a single type of thought opposed to task performance that is related to the DMN (Christoff et al., 2009), ongoing thought is a combination of multiple types of experience that relate differently to the brain and to measures of cognition (Golchert et al., 2017; Gorgolewski et al., 2014; Poerio et al., 2017; Smallwood et al., 2016; Vatansever, Bozhilova, Asherson, & Smallwood, 2018; H.-T. Wang, D. Bzdok, et al., 2018; H.-T. Wang, G. Poerio, et al., 2018). These experiences involve the interplay of a range of large-scale networks that cover the whole brain, including but not limited to the DMN.

1.3 Outcomes of Ongoing Thought

Understanding what people think about and how it varies across individuals is not only important from a theoretical standpoint. Different types of ongoing thought have been linked to a range of outcomes, both positive and negative, predominantly related to mood and task performance (Baird et al., 2012; Farley, Risko, & Kingstone, 2013; Feng, D'Mello, & Graesser, 2013; M. Franklin et al., 2014; M. S. Franklin, Mrazek, et al., 2013; Galéra et al., 2012; He, Becic, Lee, & McCarley, 2011; Kam et al., 2012; Kam, Dao, Stanciulescu, Tildesley, & Handy, 2013; Killingsworth & Gilbert, 2010; McVay & Kane, 2009, 2010, 2012a, 2012b; McVay, Kane, & Kwapil, 2009; Mooneyham & Schooler, 2013; Mrazek, Franklin, Phillips, Baird, & Schooler, 2013; Mrazek et al., 2012; Ottaviani & Couyoumdjian, 2013; Poerio, Totterdell, & Miles, 2013; Qu et al., 2015; Robison & Unsworth, 2015; Ruby, Smallwood, Engen, et al., 2013; Seli, Carriere, & Smilek, 2015; Seli, Smallwood, Cheyne, & Smilek, 2015; Smallwood & Andrews-Hanna, 2013; Smallwood, Beach, Schooler, & Handy, 2008; Smallwood, Fishman, & Schooler, 2007; Smallwood, Fitzgerald, Miles, & Phillips, 2009; Smallwood & O'Connor, 2011; Smallwood, O'Connor, Sudbery, & Obonsawin, 2007; Smallwood & Schooler, 2015; Smeekens & Kane, 2016; H.-T. Wang, G. Poerio, et al., 2018; Welhaf et al., 2019; Yamaoka & Yukawa, 2019; Zedelius & Schooler, 2015). Also, aberrant thought types, such as rumination and hallucinations are hallmarks of various psychiatric and neurodevelopmental disorders (Larkin, 1979; Nolen-Hoeksema, 2000; Papageorgiou & Wells, 2004). This section will outline what we know about the outcomes of ongoing thought, and will show how viewing experience as multi-dimensional in nature helps to understand the variance in these outcomes. It will finish by highlighting the importance of context in understanding how even the same dimension of experience can have opposing outcomes.

1.3.1 Mood and Creativity

Mind wandering in general has been related to negative mood (Killingsworth & Gilbert, 2010; Smallwood, O'Connor, et al., 2007), and although causality is hard to establish, research using lag analysis suggests it may be the thoughts causing the change in mood (Killingsworth & Gilbert, 2010). Alternatively, the induction of negative mood has also been shown to lead to increased mind wandering (Smallwood, Fitzgerald, et al., 2009; Smallwood & O'Connor, 2011). Within 'mind wandering',

different dimensions of ongoing thought have been related to different outcomes. Thinking about the past has been linked more strongly to unhappiness than thinking about the future (Poerio et al., 2013; Ruby, Smallwood, Engen, et al., 2013; Smallwood & O'Connor, 2011). In fact, certain types of future thinking, known as episodic future simulation, can reduce anxiety (Schacter, Addis, & Buckner, 2008) and increase altruism (Gaesser & Schacter, 2014). Mind wandering has also been linked to improved planning and problem solving (Baird et al., 2012), especially in social situations (Ruby, Smallwood, Sackur, & Singer, 2013). Furthermore, while repetitive and ruminative thoughts are a hallmark of disorders such as anxiety and depression (Nolen-Hoeksema, 2000; Ottaviani & Couyoumdjian, 2013; Ottaviani, Shapiro, & Couyoumdjian, 2013; Papageorgiou & Wells, 2004), interesting thoughts have been related to positive mood (M. S. Franklin, Mrazek, et al., 2013), and mind wandering has been shown to improve creativity (Baird et al., 2012). Crucially, daydreaming propensity was predictive of finding more unusual uses for objects, but more thoughts about the task itself was not, suggesting an overall link between task-unrelated thoughts and the creative process. In the Wang et al. (2018) study previously mentioned, the positive habitual dimension of thought was related to well-being, whereas spontaneous off-task thoughts were simultaneously related to affective disturbance and creativity. A recent study expanded on these relationships and found that mind wandering was related to finding more creative solution to problems, but that this in turn caused more negative affect (Yamaoka & Yukawa, 2019). These studies highlight the importance of accounting for the varied nature of ongoing thought when attempting to understand its outcomes, and show that ongoing thought can have both positive and negative consequences on mood.

1.3.2 Psychopathology

Types of ongoing thought are also characteristic of clinical disorders, with differences found in depression (Nolen-Hoeksema, 2000; Ottaviani et al., 2015; Papageorgiou & Wells, 2004) and anxiety (Makovac et al., 2019; Makovac et al., 2018), as well as borderline personality disorder (Kanske et al., 2016), post-traumatic stress disorder (PTSD) (Greenberg, 1995), obsessive compulsive disorder (OCD) (Julien, O'Connor, & Aardema, 2007; Seli, Risko, Purdon, & Smilek, 2017), autism spectrum disorders (ASD) (Solomon, Ozonoff, Carter, & Caplan, 2008), and even in an extreme form during psychosis (Larkin, 1979; Shin et al., 2015). These differences

are predominantly driven by an increased negative valence of thoughts and pervasiveness (Marchetti, Koster, Klinger, & Alloy, 2016). Healthy individuals are generally able to limit negative thoughts and or transform them into something more positive as they mature (John & Gross, 2004), known as reappraisal (McRae, Ochsner, Mauss, Gabrieli, & Gross, 2008) or substitution (Hertel & Calcaterra, 2005). These strategies are deficient in depression (Campbell-Sills, Barlow, Brown, & Hofmann, 2006), anxiety (Aldao, Nolen-Hoeksema, & Schweizer, 2010), OCD (Amir, Cashman, & Foa, 1997), and PTSD (Ehring & Quack, 2010), suggesting that controlling what you think about is an essential feature of healthy psychological functioning. The differences in this ability to control the contents of your thoughts, and therefore manage the problematic outcomes of certain types of thinking, is known as the "content regulation hypothesis" (Andrews-Hanna, Smallwood, & Spreng, 2014). While it has been hypothesised that current concerns often drive the contents of thought (Klinger, 2013), the affect and pervasiveness of these thoughts varies largely within the population. Altered ongoing thought is also a hallmark of ADHD, with studies showing that these individuals perform more "spontaneous" but not "deliberate" mind wandering (Seli, Smallwood, et al., 2015), suggesting they have more task-unrelated thoughts in situations where they want to pay attention to the task. A further study showed more mind wandering in general in these individuals, as well as more mind wandering that they rated as "detrimental" to the task they were performing (M. Franklin et al., 2014). More recently, a study using MDES found that ADHD symptoms in a neurotypical population were specifically related to the inability to maintain task-related detail (rather than off-task thought per se) (Vatansever et al., 2018). The variation in the types of thought people engage in clearly has an important effect on psychological well-being, and these studies again highlight the importance of viewing ongoing thought as multi-dimensional in nature.

1.3.3 Task Performance

Certain types of ongoing thought, particularly those referred to as 'mind wandering' are consistently associated with negative outcomes on task performance that transfer to education and daily life. This negative impact provides an incentive for researchers to assess the impact of task-unrelated thought during reading or lectures. Mind wandering has been shown to have a negative impact on performance in these situations (Dixon & Bortolussi, 2013; Farley et al., 2013; Feng et al., 2013; M. S.

Franklin et al., 2011; Jackson & Balota, 2012; McVay & Kane, 2012a; J. W. Schooler, 2004; Smallwood, McSpadden, & Schooler, 2008; Szpunar, Khan, & Schacter, 2013; Unsworth & McMillan, 2013), and the potential overall cost of off-task thoughts in education is proposed to be high (Smallwood, Fishman, et al., 2007). One study found that levels of task-unrelated thought during tests in the laboratory were predictive of SAT performance, highlighting the potential long term impact of failing to inhibit these thoughts when external attention is important (Mrazek et al., 2012). These studies show that certain types of ongoing thought are related to poor performance on tasks that generalises to difficulties in daily life (Kane et al., 2007), particularly in educational settings.

1.3.4 The Importance of Context

So far, variation in ongoing thought has been linked to both negative and positive mood, poor task performance and creativity. While some of this variation has already been explained as due to the varied nature of ongoing thought, in some cases the same types of thought lead to opposing outcomes across different studies. This is particularly true of off-task thought, which is characterised by its negative impact on task performance (Kane et al., 2007), but also shows links to creativity (Baird et al., 2012; Smeekens & Kane, 2016) and intelligence (H.-T. Wang, D. Bzdok, et al., 2018; Welhaf et al., 2019). The cause of this heterogeneity is largely related to context. Cognitive psychology predominantly studies processing using cognitively demanding tasks (I. H. Robertson, Manly, Andrade, Baddeley, & Yiend, 1997). During these tasks, off-task thought is detrimental to performance (Engle & Kane, 2004; Kane et al., 2007; McVay & Kane, 2009, 2010, 2012a, 2012b; McVay et al., 2009). This is due to the fact that there are limited cognitive resources available to cognition, so that there is a limit to the information that can be accessed at any moment (Smallwood, 2010). This means there is a trade-off in attention, including between that which is directed internally and that which is external. This means that ongoing thought needs to be regulated to fit the demands posed by the external environment, in order to minimise the negative consequences. This is known as the context regulation hypothesis (Andrews-Hanna et al., 2014). In this way, the negative outcomes are not so much a result of the type of thinking itself, rather the inability to properly prioritise processing in line with the demands of the environment. It is unclear the extent to which dimensions of experience other than task-relatedness also vary across task contexts:

previous research using the paradigm in this thesis suggests that both the level of detail and modality of thoughts also vary depending on the task during which experience is measured (Sormaz et al., 2018; Vatansever et al., 2018). It is clear that in order to understand the outcomes of ongoing thought, it is vital to take into account the context in which they are occurring, and measuring thought using MDES in a range of contexts will provide important clarification about the role of context in future research.

Similarly, many of the negative outcomes of ongoing thought that relate to mood are not a result of the thoughts themselves, rather they are related to the inability to limit the time spent in certain states to when they are needed for "task performance" (which could include thinking through a problem). For example, it is not an indicator of psychopathology if you think a lot about an upcoming exam, and if you can use those thoughts productively to improve performance it is adaptive. The most useful thoughts are likely to occur in defined periods and cover a range of topics that may be included in the test. However, spending a whole day thinking about the same exact definition over and over again is not likely to benefit performance, and if it comes with negative mood and feelings of inadequacy it is likely to be detrimental. Worrying in a way that is repetitive, negative, and hard to control is known as rumination, and is a hallmark of mood disorders (Nolen-Hoeksema, 2000; Papageorgiou & Wells, 2004). Even types of thinking that are themselves positive can lead to negative outcomes, if time is spent engaging with them that would be better used maintaining states that are needed for daily function. For example, some forms of daydreaming, if they occur over extensive periods and negatively impact normal functioning, are characteristic of a disorder known as 'maladaptive daydreaming' (Bigelsen, Lehrfeld, Jopp, & Somer, 2016; Schupak & Rosenthal, 2009). In the laboratory, levels of task-unrelated thoughts appear to increase over time as tasks get more boring (Smallwood, Obonsawin, & Reid, 2002), or automatic (Teasdale et al., 1995), showing that in healthy individuals spontaneous thought processes are inherently dynamic, potentially providing a means by which thoughts can be limited to when they are most useful. It is an open question how these processes are regulated on this time scale and how they relate to cognitive processing. However, it is clear that the ability to maintain mental states appropriately is essential to minimising the negative consequences of ongoing thought (Smallwood & Schooler, 2015). The inability to properly disengage with certain types of thought

when they become harmful is another leading cause of the negative outcomes associated with ongoing thought (Julien et al., 2007; Nolen-Hoeksema, 2000; Papageorgiou & Wells, 2004; Seli et al., 2017).

This section has provided an overview of the outcomes of ongoing thought. These outcomes are varied and can be both positive, including relationships to positive mood (M. S. Franklin, Mrazek, et al., 2013) and creativity (Baird et al., 2012), or negative, related to negative mood (Killingsworth & Gilbert, 2010) and performance errors (Kane et al., 2007). In extreme cases, certain types of thinking, including hallucinations and rumination are characteristic of various psychiatric and neurodevelopmental disorders (M. Franklin et al., 2014; M. S. Franklin et al., 2017; Julien et al., 2007; Larkin, 1979; Nolen-Hoeksema, 2000; Seli, Smallwood, et al., 2015; Solomon et al., 2008). It is vitally important to understand the processes involved in ongoing thought in order to help clarify how individuals can avoid the negative consequences of their thoughts. While some aspects of this problem can be solved by avoiding certain types of ongoing thought, the same dimensions of experience can have opposing outcomes, shown by the relationship of task-unrelated thought to both executive failure (Kane et al., 2007) and creativity (Baird et al., 2012). It is essential to consider the external context within which thoughts occur to understand their outcomes: in order to minimise the negative consequences of ongoing thought it is necessary to prioritise specific dimensions, such as those that are internal in nature, only when the situation allows it (Andrews-Hanna et al., 2014).

1.4 A State Framework

One account of ongoing thought suggests that it can be understood as a sequence of trains of thought that, once initiated, can be maintained by the engagement of domain general neurocognitive processes – the so-called process occurrence framework (Smallwood, 2013a). The separation of dynamic experience into these sustained trains of thought and their initial occurrence provides a useful model for researching the mechanisms of internal experience. In this way, ongoing thought is divided into two elements: moments where attention is switching between an internal and an external focus of attention, and moments where attention is being maintained externally or internally. However, states can be defined along more axes than just whether they are externally or internally focused, as has been shown by the

studies using decomposition techniques above (Konishi et al., 2017; Poerio et al., 2017; Ruby, Smallwood, Engen, et al., 2013; Sormaz et al., 2018). A state framework builds on this model by suggesting that each moment in time can be understood as a point in a multi-dimensional state space. For example, at a specific point in time a person could be engaging in a thought about what they are going to have for dinner. This specific thought may be unique in its exact make-up; the person is unlikely to have had the exact same thought in the exact same way before. Similarly, their brain will show a unique pattern of activity. However, using experience sampling followed by dimensionality reduction techniques an estimation of this state along a more manageable number of dimensions can be obtained. Using the four dimensions captured by previous studies (Poerio et al., 2017; Sormaz et al., 2018; Vatansever et al., 2018), this state could be detailed, off-task, in words, and positive in emotional valence. Temporally, experience would then be divided into time periods where the state of the individual is remaining within the same area of state space, described as state maintenance, and time periods where the person is moving through state space. These transitions could occur along one dimension, in this case a move to a detailed, word-based, positively valenced task state, or multiple dimensions to a completely different state.

This framework is useful because it removes the need for strict definitions for specific states (Seli, Kane, et al., 2018), which can instead be described empirically, and does not tend towards definitions based on absence (e.g. mind wandering as the absence of task focus). This is necessary especially when studying these processes using fMRI: contrasting specific task states with the absence of these states is likely to identify neurocognitive processes in a manner that makes it impossible to establish their true role, as has been the case with the DMN (Christoff et al., 2009; Crittenden et al., 2015). It also continues to separate the neurocognitive processes engaged during specific states from those that enable moving between states. This is theoretically necessary because the majority of methods in cognitive psychology are biased towards identifying the processes involved in state maintenance, and these should not be confused with those engaged during the more difficult to study state transitions (Smallwood, 2013a). Once a state has been located in this space, and it has been determined whether the analysis is likely to have identified a maintenance

or transition period, it is then possible to delineate the neurocognitive systems involved in a more interpretable manner.

fMRI provides a comprehensive measurement of continuous processing during ongoing thought that can be used to understand the movement of the mind through this state space. However, while traditional cluster correction methods used in fMRI are essential to ensure the minimisation of type 1 error (Eklund, Nichols, & Knutsson, 2016), they tend towards producing single regions or clusters of regions as results in fMRI studies. Recently, there has been a shift away from viewing the brain through a localizationist lens that assigns roles to regions and towards understanding the brain in terms of networks (Thomas Yeo et al., 2011) or functional hierarchies (Margulies et al., 2016). Using these organisational principles to reduce the dimensions of whole brain patterns is useful for enabling a better understanding of fMRI results and consolidating seemingly convergent results into coherent theories of brain function (Eickhoff, Yeo, & Genon, 2018). A study using dimensionality reduction techniques on fMRI data during task performance found that a low-dimensional manifold could be used to explain the reorganisation that takes place during task performance (Shine et al., 2019). They found that flexibly reorganising neural activity along this dimension was related to accuracy on the task as well as fluid intelligence. Similarly, a study using the functional hierarchies from Magulies et al. (2016) to characterise states identified during ongoing thought found that these states largely existed to the extremes of this gradient space (Karapanagiotidis, Vidaurre, et al., 2019). They also found that the gradient explaining the third most variance in Margulies et al. (2016) was the most strongly related to measures of experience taken at the end of the resting state scan. This gradient is anchored at one end by regions active during external task performance, sometimes referred to as the "multiple demand network" (Duncan, 2010), and at the other by the DMN. Specifically, more "task-like" states (characterised by activity in multiple demand network regions) related to future problem-solving and more "rest-like" states (DMN activity) related to spontaneous, self-generated thought. Interestingly, the pattern of brain organisation identified in this "gradient" closely resembles the "manifold" that is re-organised during task performance in Shine et al. (2019), suggesting that these techniques are providing meaningful evidence for a consistent framework of state transitions in the brain. These studies provide evidence

for the existence of a state space through which experience can be meaningfully understood, measureable by fMRI as well as experience sampling.

These methods are promising, but few studies have so far utilised them to gain a picture of how the brain moves through state space. Information gained from more traditional approaches that assume a more modular view of neurocognitive processing is still vital to informing these novel methods and furthering our understanding of how states are maintained and transitioned between. These methods leverage two main aspects of experience in order to probe the neurocognitive basis of ongoing thought. The first relates to the fact that ongoing thought involves the engagement of domain general component processes that can be measured experimentally using cognitive tasks or fMRI (Poerio et al., 2017). Individuals who engage these processes effectively during tasks are also able to engage them in the same way during ongoing thought. For example, participants with low levels of working memory capacity as measured during a task have less working memory capacity to allocate during ongoing thought (Kane et al., 2007; McVay & Kane, 2009, 2010, 2012a, 2012b; McVay et al., 2009). This explains why they are less able to maintain external task states during difficult tasks and engage in less off-task thought during easy tasks (Levinson, Smallwood, & Davidson, 2012; Rummel & Boywitt, 2014). In general, therefore, ongoing thought can be captured using experience sampling and then related to measures of cognition taken during task performance across participants in order to understand which processes are involved.

The second is conceptually more simple, and involves the use of fMRI during ongoing thought to capture the brain activity that relates to processing during each state in-the-moment. The domain general processes that are engaged during the period of ongoing thought can be established by comparing the specific brain regions or networks that are active to their known involvement in more specific tasks, ideally using large-scale meta-analytic tools (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011). For example, if regions in the brain that are typically active during executive control processes are also engaged during moments of off-task thought, this would suggest that these processes are engaged in maintaining this internal state (Christoff et al., 2009). This section will use a state framework to review evidence from methods that relate ongoing thought to cognitive processes to elaborate what we know about the systems engaged during ongoing thought, starting with those involved in

periods of state maintenance. It will then explain why these approaches are less well-suited for understanding state transitions, before elaborating how researchers have attempted to overcome this difficulty and what they have discovered about the neurocognitive processes involved in state transitions. Thinking of ongoing thought this way can help to reconcile some of the debates of the literature, specifically those around the role of executive control (McVay & Kane, 2010; Smallwood, 2010, 2013a) and the DMN (Andrews-Hanna et al., 2014; Crittenden et al., 2015; Konishi et al., 2015; Margulies et al., 2016; V. Smith, Mitchell, & Duncan, 2018; R Nathan Spreng & Grady, 2010; Tylén et al., 2015) in ongoing thought.

1.4.1 State Maintenance

During sustained periods, states are maintained by component processes, some general and some specific to the state: for example, whether it is internally or externally focused, or its content. One process that is unique to internal states, but potentially ubiquitous across them, is perceptual decoupling (Handy & Kam, 2015; Smallwood, Beach, et al., 2008), the isolation of mental content against external input. Two processes that appear to be shared between internal and external states are executive control (Levinson et al., 2012; Smallwood, Brown, Baird, & Schooler, 2012) and sensory processing (Reddy, Tsuchiya, & Serre, 2010; Slotnick, Thompson, & Kosslyn, 2012). It is not clear whether these more general processes occur in the same way during external and internal states, but there is evidence that the cognitive (Levinson et al., 2012) and neural systems can be overlapping (Reddy et al., 2010). This section will examine the evidence for the role of perceptual decoupling, executive control, and sensory processing in the maintenance of states. It will also suggest that a final process, the ability to monitor the external environment, is also essential to the ability to maintain internal states effectively for organisms living in a dynamic environment.

1.4.1.1 Perceptual Decoupling

The primary process that distinguishes internal from external states is perceptual decoupling. This dampening of external input to consciousness (Smallwood, 2013a) during internal states has been confirmed to exist by multiple lines of research. Studies using pulmometry have showed that changes in pupil diameter are decoupled from task events during mind wandering episodes (Kang, Huffer, &

Wheatley, 2014; Smallwood et al., 2011). A study looking at the P3 event-related potential (ERP) component of the electroencephalogram (EEG) signal that is thought to represent cognitive analysis found attenuation in intervals immediately preceding participant reported mind wandering, as well as those before performance errors, suggesting a common mechanism (Kam et al., 2013). This result was replicated, and it was additionally found that the P3 was diminished during mind wandering whether the target was task-relevant (oddball) or irrelevant (distractor) (Barron et al., 2011). This suggests that it relates more generally to internal processing rather than just performance error. O'Connell and colleagues expanded on these results, and found that an ERP component related to stimulus anticipation was also reduced prior to missed targets (O'Connell et al., 2009). Finally, Kam and colleagues extended this same analysis to painful (and therefore salient) stimuli, and found equivalent results in both the P3 ERP and behavioural ratings of pain (Kam, Xu, & Handy, 2014).

In addition to these results using EEG, several studies have used fMRI to study this process. One paradigm that is particularly useful for understanding the differences between internal and external attention involves having participants complete alternating blocks of 0-back and 1-back conditions (Konishi et al., 2015; C. Murphy et al., 2018; C. Murphy, Wang, et al., 2019). This keeps external input constant while altering the focus that is necessary at the moment of response: in the 0-back the participant must use perceptual input to guide their decision, whereas they must focus on internal representations of the preceding trial to respond in the 1-back. Additionally, during the 0-back non-target trials can be ignored without a negative impact on task performance, encouraging more internal states in this condition. The first of these studies identified regions within the DMN as being related to decisions involving memory-guided rather than perceptually-guided decision-marking (Smallwood, Tipper, et al., 2013). Replicating this, Konishi and colleagues analysed the periods during which cognition was perceptually decoupled (responding during the 1-back and off-task periods during the 0-back) and found similar regions, also within the DMN (Konishi et al., 2015). Finally, a study by Murphy and colleagues showed that periods of remembering are characterised by increased activity in the DMN and corresponding decreases of activity in the visual cortex, providing further evidence for perceptual decoupling during internally focused thought (C. Murphy et al., 2018). These studies, alongside others showing comparable results with different ERP components

(Smallwood, Beach, et al., 2008), fMRI activity (Weissman, Roberts, Visscher, & Woldorff, 2006), and behavioural responses (Kam & Handy, 2013), demonstrate that periods when attention is focused inwards have a corresponding decrease in external input to conscious experience. One mechanism by which this may occur is through the disconnection of visual regions from external input (C. Murphy, Wang, et al., 2019), with a corresponding increase in the connectivity and activity of neural systems involved in internal experience, including the DMN (Karapanagiotidis, Jefferies, & Smallwood, 2019; Kucyi & Davis, 2014; Pearson, 2019; Sormaz et al., 2018; Weissman et al., 2006).

1.4.1.2 Executive Control

The role of executive control in maintaining states is more contested, with some earlier studies suggesting that internal states were spontaneous in nature and arose due to executive failure (Engle & Kane, 2004; Kane et al., 2007; McVay & Kane, 2009, 2010, 2012a, 2012b; McVay et al., 2009), while other results showed that executive resources could support internal states in undemanding situations (Levinson et al., 2012; Rummel & Boywitt, 2014; Smallwood, 2010, 2013a; Smallwood & Schooler, 2006). Executive control is a term that is largely used to explain attentional abilities, such as the ability to focus on task goals or working memory, and switch between focal points in a goal-driven rather than habitual manner (Engle & Kane, 2004). Working memory specifically describes the capacity for holding information temporarily for simultaneous storage and manipulation (Baddeley, 1992). In the brain, executive control has been shown to involve prefrontal and parietal brain regions (Curtis, 2006; Diwadkar, Carpenter, & Just, 2000; Klingberg, O'Sullivan, & Roland, 1997; Olesen, Westerberg, & Klingberg, 2004; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002). Network models of the brain group these regions into a frontoparietal control network (FPCN), which can be identified in brain parcellations (Thomas Yeo et al., 2011) and shows temporal coherence (Vincent, Kahn, Snyder, Raichle, & Buckner, 2008). This network is recruited during tasks, particularly when demands increase (Klingberg et al., 1997), and also allows cognition to proceed within an abstract set of rules (Cole et al., 2013).

The first study to look at the relationship between executive control and internal states found that WMC was related to better maintenance of on-task attention during

cognitively demanding tasks in daily life (Kane et al., 2007). Building on this, WMC was shown to impact performance on a sustained attention task largely through its attenuation of task-unrelated thoughts (McVay et al., 2009). This was replicated during reading, with WMC affecting comprehension through its limitation of mind wandering (McVay & Kane, 2012b). A study looking at several measures of general aptitude including WMC found that mind wandering during these tasks negatively affected participants scores (Mrazek et al., 2012). This poses a problem for attempts to link mind wandering to measures of executive control, as it means that participants that are prone to these states score lower on these measures, making the argument that mind wandering is related to poor executive control somewhat circular. Additionally, it is clear that internal thought in non-demanding situations does not carry the same negative relationship to executive control. In fact, allowing mind wandering to occur during simple tasks has been shown to be an indicator of improved executive control (Levinson et al., 2012). As well as reducing task-unrelated thoughts in demanding situations, participants with greater WMC were found to be more flexible in their coordination of on- and off-task thoughts, allowing them to flexibly adjust their thoughts to situational demands (Rummel & Boywitt, 2014). Engaging in internal states during simple tasks has also been related to the ability to delay gratification (Bernhardt et al., 2014; M. S. Franklin, Mrazek, et al., 2013) and produce creative answers during the unusual uses task (Baird et al., 2012). This highlights the complex relationship between off-task thought and executive control, and indicates the importance of context. Separating ongoing thought into states that are maintained and transitioned between helps to resolve some of this confusion, and suggests that the maintenance of a specific state requires executive resources whether it is internal or external in nature.

Within a state framework, executive failure may lead to a transition away from an external state that was being maintained, but the subsequent maintenance of this internal state requires support in the same way as the preceding task-focused state in order to continue uninterrupted (Smallwood, 2013a). The failure to maintain a state, whether it is internal or involves task focus, could be caused be executive failure, but all states require certain resources to sustain them over extended periods, some of which may be executive depending on the nature of the state. It is unclear if the resources needed to sustain internal and external states are identical, however, they

likely rely on similar domain general processes. One study found that lesions to the lateral cortex caused reductions in neural signals related to processing both internal and external attention (Kam, Solbakk, Endestad, Meling, & Knight, 2018). Another study found that these signals are identifiable in adjacent but non-overlapping parts of the cortex (Sestieri, Shulman, & Corbetta, 2010). Pre-frontal and parietal regions engaged during executive control (Dosenbach et al., 2007; Jurado & Rosselli, 2007; Seeley et al., 2007) are consistently found to be activated in studies on mind wandering (K. C. Fox, Spreng, Ellamil, Andrews-Hanna, & Christoff, 2015), and co-activation of these regions with regions of the DMN was shown to predict attentional lapses during an externally focused task (Mittner et al., 2014). Taken as a whole, these results suggest that both internal and external states require support from executive control systems.

1.4.1.3 Sensory Processing

State maintenance also requires sensory processing to provide states with perceptual information, and studies looking at mental imagery have shown that internal states recruit similar sensory regions to perception. Motor imagery has been shown to involve activation in motor regions (Pfurtscheller & Neuper, 1997; Porro et al., 1996), visual imagination activates visual regions (Ganis, Thompson, & Kosslyn, 2004), and these activations carry information about the type of visual information being imagined in the same way as in studies looking directly at perception (Formisano et al., 2002; O'Craven & Kanwisher, 2000; Reddy et al., 2010). Internal states could recruit these cognitive processes and their associated neural representations in a content-dependent manner in order to infuse the internal state with perceptual details. The DMN likely plays a role in coordinating and integrating these distributed representations into mental scenes, enabled by the fact that it includes many hub regions of the brain with far reaching connections (Tomasi & Volkow, 2011), and by its position at the opposite end of a principal gradient of brain organisation to sensory regions (Margulies et al., 2016). It has been shown to co-activate with (Thakral, Benoit, & Schacter, 2017) and increase connectivity to (Schlegel et al., 2013) visual regions during imagination/visual imagery. Cross-sectionally, resting state connectivity between the DMN and visual areas was related to the content of future thought (Villena-Gonzalez et al., 2018). This DMN region in turn was connected to regions across the brain including the core of the DMN, allowing a mechanism for the

incorporation of information from sensory regions into a consistent mental scene within the DMN. It is unclear how this process differs between internal and external states: it may be that this difference relies on the direction of information flow, a theory that is supported by evidence from both fMRI (Dijkstra, Zeidman, Ondobaka, van Gerven, & Friston, 2017) and EEG (Dentico et al., 2014).

1.4.1.4 Monitoring

This section has evaluated the evidence for the role of a range of neurocognitive processes involved in maintaining states. These processes are differentially engaged depending on the needs of the external context in order to minimise the negative consequences associated primarily with performance errors (Levinson et al., 2012; Rummel & Boywitt, 2014). This context regulation requires a mechanism that provides information about the external context so that states can be maintained appropriately given the needs of the situation. This could rely on conscious processes linked to meta-awareness/cognition (thinking about one's own thoughts (Baird, Smallwood, Gorgolewski, & Margulies, 2013; M. Franklin et al., 2014; M. S. Franklin et al., 2017; J. Schooler & Schreiber, 2004; J. W. Schooler, 2002, 2004; J. W. Schooler et al., 2011)) or lower level processing related to salience (Herry et al., 2007; Kim et al., 2011; Peck & Salzman, 2014; Pessoa & Adolphs, 2010; Wiech et al., 2010). While external input has been shown to be attenuated during internal states, several processes related to external information have been shown to remain stable. These include the processing of particularly salient events (Kam et al., 2013) and task-switching (Kam & Handy, 2014). It is important that salient events can disrupt internal thought as this could allow the individual to re-engage with sensory input in cases where they may be at risk. These findings suggest a process by which the environment is monitored during states so that information can be prioritised given the nature of the situation, which also allows states to transition if this situation changes.

Overall, states are maintained by a range of neurocognitive processes, some of which are unique to internal states and some of which appear more general. Perceptual decoupling describes the attenuation of external input during internal states that isolates them and is the cause of the relationship between mind wandering and performance errors (Kam & Handy, 2013). These are caused by limitations to the resources that are shared between internal and external states (Smallwood, 2010).

These resources include those related to executive control (Levinson et al., 2012), as well as lower level perceptual processes. These can either be coupled to external input or can be integrated into internal states to provide content to imagery (Reddy et al., 2010). In order to ensure these resources are allocated appropriately, a process of monitoring needs to take place that provides information about the external context in a dynamic way and allows for transitions to occur when necessary.

1.4.2 State Transitions

While we understand many of the processes and brain networks that are engaged during states, it is less clear how transitions between states take place. This is partly because the methods used to study ongoing thought are predominantly focused on measuring experience at specific time points or over extended periods: the exact moment a state emerges in the brain is difficult to pinpoint. This 'ignition' is thought to relate to the hippocampus (Smallwood, 2013a), as it is theorised that the same system that is used to store and consolidate representations about the past would be involved in producing novel combinations of experience for predictions about the future or imaginings (Buckner, 2010). While the hippocampus is indeed involved in imagining the future (Schacter, Addis, & Buckner, 2007), it is unclear whether it is activated at the moment of thought initiation. Studies using single cell recordings have shown that neurons in the hippocampus that responded during movie-watching fire at a faster rate during spontaneous recall of the same movie clip (Gelbard-Sagiv, Mukamel, Harel, Malach, & Fried, 2008). While theoretically important, it is not necessary to perfectly define the moment a state emerges in order to probe the processes involved in state transitions. Thinking in terms of states, transition can be defined as any significant movement in state space, meaning experimental designs that allow participants to move between different states can be leveraged to understand these dynamics. This is especially true when these designs are combined with a continuous measure of brain activity such as fMRI. This section will examine a range of task-based fMRI studies that have been specifically designed to probe state transitions. It will also give an overview of studies that combine fMRI with behavioural markers that give insight into the participants' state to better capture state transitions. Following that, it will evaluate novel dynamic approaches to analysing fMRI data, suggesting how they could be adapted to enable a better understanding of state transitions.

1.4.2.1 Evidence from Task-based Approaches

Several studies have measured states behaviourally and worked backwards in an attempt to probe changes in brain activity that likely took place during the transition to that state. A study by Hasenkamp and colleagues asked experienced meditators to focus on their breath, and push a button when they realised their attention had wandered, then refocus on the breath (Hasenkamp et al., 2012). They then created an analytical model that considered four (3 second) phases of mind wandering: a mind wandering baseline (prior to indicated awareness), aware (centred on the button press), shifting attention, and then focusing back on the breath. They found that during awareness, activation in the ventral attention network (VAN), or salience network was relatively strong, consistent with studies that show that this network plays a role in state monitoring (Eckert et al., 2009) and task-set maintenance (Dosenbach et al., 2007). During the shift in attention, regions in both the FPCN and dorsal attention network (DAN) were active, consistent with their roles in rule-based cognition (Cole et al., 2013) and top-down attentional control (Corbetta, Patel, & Shulman, 2008), respectively. During the mind wandering phase, regions in the DMN were identified, but only when contrasting it against the shifting phase. The use of experienced meditators tasked with monitoring their own thought is likely to alter the mechanisms of state transition, which in this case involve shifts towards a relatively unique state with a bodily focus. However, this study provides insight into the role of several networks in state transitions, pointing to a role for the VAN in monitoring and awareness, and for the FPCN and DAN during transition phases.

A similar study also using meditation practitioners had them perform 30 second blocks of either thought monitoring (internally direction) or word monitoring (externally directed to words on a screen) (Ellamil et al., 2016). They modelled their data so that a thought was considered to have arisen 4 seconds prior to the button press. The inclusion of an externally focused condition allowed them to directly compare brain activity during transitions to internal states to those involved in shifts to external states. Their analysis identified a set of regions including those in the DMN, as well as bilateral hippocampi, bilateral insular cortices and dorsal anterior cingulate cortex (ACC; within the VAN). Further analysis on the time courses of these activations showed that activity in the hippocampi, posterior DMN, and VAN (insula and ACC) was higher preceding the button press, decreasing once it had been pressed. While this study

benefitted from an external attention comparison that suggests these results are specific to transitions to internal states, it is also limited by the need for the participant to monitor their thoughts and indicate the point of transition once it has entered awareness. Furthermore, it is hard to say whether experienced meditators monitor their thoughts and shift between states in the same manner as the general population. Nonetheless, this study provides further insight into this process of state transition, and suggests that an array of brain regions, from multiple networks, including the hippocampus and VAN, is important for transitioning to internal states. It further suggests that there may be differences between the processes involved in transitions depending on the direction through which the individual is moving in state space.

A promising avenue to build on this evidence involves studying state transitions using MDES with fMRI, to enable a more detailed picture of different states beyond just internal vs. external (Christoff et al., 2009; Stawarczyk, Majerus, Maquet, et al., 2011). Adding information about the content of thoughts would allow researchers to capitalise on the fact that states and their associated neural patterns can be better characterised. Knowing the pattern that represents a certain thought would allow researchers to track this pattern's emergence in the brain. Related analyses have been done to successfully decode visual imagery during wakefulness (Kamitani & Tong, 2005; Miyawaki et al., 2008) and sleep (Horikawa & Kamitani, 2017; Horikawa, Tamaki, Miyawaki, & Kamitani, 2013). In this study (Horikawa et al., 2013), models trained on stimulus-induced fMRI data in visual cortices accurately identified dream contents obtained from verbal reports. Characterising the brain activity patterns related to specific states using MDES and fMRI could enable detection of neural signatures of thought content that would allow tracking of these patterns over time within a time course of brain activity.

1.4.2.2 Studies using Behavioural Markers

A difficulty of understanding state transitions using experience sampling is that this method provides a snapshot of the participant's state at a specific moment in time. To probe the mechanisms of state transitions, one has to estimate when the state emerged, working backwards from the experience sampling probe. Asking the participant about their current state also inherently changes it, and requires them to perform a judgement about their state immediately prior to the moment of asking that

relies on self-report and memory (Smallwood & Schooler, 2015). The best chance of understanding transitions in ongoing thought states may lie in a combination of covert behavioural measures and neuroimaging. These measures give a second real-time indicator of the participant's state that is not biased by the requirement for monitoring. Several studies have shown that mind wandering causes changes in pupillometry (M. S. Franklin, Broadway, et al., 2013; Smallwood et al., 2011), and physiological markers such as skin conductance (Frith & Allen, 1983) and heart rate (Smallwood, O'Connor, et al., 2007). Studies using machine learning techniques have shown that it is feasible to detect transitions to internal states using these physiological signals (Blanchard, Bixler, Joyce, & D'Mello, 2014), as well as eye-gaze during movie-watching (Bixler, Mills, Wang, & D'Mello, 2015) and reading (Bixler & D'Mello, 2014, 2015, 2016). Using similar techniques alongside fMRI scanning would allow the identification of neural markers of specific states that would allow their emergence to be tracked in the brain in state space.

1.4.2.3 Dynamic fMRI Analyses

Another promising approach to studying state transitions is to look for dynamic patterns within the neural information itself in a data-driven fashion. One such approach uses hidden Markov modelling to look for states within time series of neural activity. This has been successfully applied to magnetoencephalography data (Vidaurre et al., 2016) and fMRI data (Karapanagiotidis, Vidaurre, et al., 2019). This second study showed that large-scale brain organisation can be used to create a state space into which data-driven neural patterns can be placed. This provides a useful model for understanding how the brain moves through state space, but further analyses would be needed to identify the processes directly involved in state transitions, as this type of modelling divides the data collection period into segments that capture maximum difference in states. This biases it towards identifying periods of state maintenance. However, additional analyses can be performed at the boundaries of these periods that may give insight into state transitions. Other computational approaches have attempted to identify aspects of neural dynamics that predict changes in brain state, specifically between integrated and segregated forms. There is some evidence that task performance causes neural integration (Vatansever, Menon, Manktelow, Sahakian, & Stamatakis, 2015), particularly as the time within the task state progresses (Fransson, Schiffler, & Thompson, 2018). Changes in neural

"gain" (mediated by neuromodulatory nuclei related to the noradrenaline system) have been shown to affect the likelihood of state transition (Shine, Aburn, Breakspear, & Poldrack, 2018) and could be a potential causal mechanism for initiating state transitions. Having such a mechanism, that is potentially linked to internal cyclical physiological processes, would provide a dynamic input to the system that ensures effective state transitions. Hierarchical systems have been proposed to exist throughout the central nervous system to provide homeostasis to neural functioning to allow humans to function within an ever-changing environment (R. Smith, Thayer, Khalsa, & Lane, 2017). Understanding how the different levels of this hierarchy interact in both healthy and disordered functioning will be essential to fully unravel the mechanisms involved in state dynamics.

Overall, these studies suggest that a range of large-scale brain networks and subcortical structures are involved in state transitions. The VAN seems to play a significant role in state monitoring (Hasenkamp et al., 2012), with the FPCN and DAN more involved during state transitions (Ellamil et al., 2016; Hasenkamp et al., 2012). However, these studies involve experienced meditators in paradigms that require continuous monitoring that is likely to affect the way that state transition occurs and reduce the generalisability of these findings. Moving these types of analyses into a more representative population in a paradigm that attempts to model transitions more naturally could help improve our knowledge of these processes. Studies have shown that covert behavioural markers are indicators of state transitions (M. S. Franklin, Broadway, et al., 2013; Frith & Allen, 1983; Konishi et al., 2017; Smallwood et al., 2011), and combining these with fMRI is another fruitful avenue for studying state transitions. Data-driven approaches to understanding how the brain reorganises at rest and during tasks also represent a promising avenue for probing state transitions. These studies suggest that state transitions involve whole-brain reorganisations in a relatively low-dimensional space (Karapanagiotidis, Vidaurre, et al., 2019; Shine et al., 2019), and that these may be driven by neuromodulatory systems (Shine et al., 2018) as part of a complex hierarchy within the central nervous system that incorporates information about internal physiology as well as the external environment to guide state transitions (R. Smith et al., 2017).

1.5 Conclusion

This introductory chapter has reviewed the literature on ongoing thought to highlight three main factors that are essential to understanding the systems it involves and its varied outcomes:

- Ongoing thought is heterogeneous, consisting of dimensions that can be reliably identified using data-driven methods applied to experience sampling data and that relate differently to neurocognitive measures and outcomes (Gorgolewski et al., 2014; Poerio et al., 2017; Vatansever et al., 2018; H.-T. Wang, D. Bzdok, et al., 2018; H.-T. Wang, G. Poerio, et al., 2018).

- Context is vital to understanding why specific states emerge, and why similar dimensions of experience can have opposing outcomes depending on the external situation (McVay & Kane, 2010; Smallwood, 2010, 2013a; Smallwood & Andrews-Hanna, 2013).

- Ongoing thought is dynamic, and these dynamics rely on distinct processes to those involved in maintaining states (Dosenbach et al., 2007; Ellamil et al., 2016; Hasenkamp et al., 2012; Smallwood, 2013a).

In addition to being practically useful for explaining how ongoing thought can have such varied outcomes, these factors are also essential to understanding the processes involved in ongoing thought and reconciling debates in the field, such as the role of executive function (McVay & Kane, 2010; Smallwood, 2010, 2013a; Smallwood & Schooler, 2006) and the DMN (Andrews-Hanna et al., 2014; Crittenden et al., 2015; Elton & Gao, 2015; Konishi et al., 2015; Margulies et al., 2016; Mars et al., 2012; Raichle et al., 2001; V. Smith et al., 2018; R Nathan Spreng & Grady, 2010; Vatansever, Menon, & Stamatakis, 2017). This chapter proposed a model that separates ongoing thought into states that exist within a multi-dimensional space, and are maintained and transitioned between over time. Using this model, it elaborated research that suggests a role for perceptual decoupling in maintaining internal states (Kam & Handy, 2013; C. Murphy et al., 2018; J. W. Schooler et al., 2011; Smallwood, 2013b; Smallwood et al., 2011; Smallwood, Tipper, et al., 2013), and roles for both executive control (Levinson et al., 2012; Rummel & Boywitt, 2014; Smallwood, Brown, Baird, & Schooler, 2012; R Nathan Spreng, Stevens, Chamberlain, Gilmore, &

Schacter, 2010) and sensory processing (Ganis et al., 2004; Horikawa et al., 2013; Karapanagiotidis, Jefferies, et al., 2019; Mellet et al., 2000; Pearson, 2019; Pfurtscheller & Neuper, 1997; Reddy et al., 2010; Slotnick et al., 2012) in maintaining states more generally. It also pointed out the need for an additional process of monitoring that is essential for ensuring state transitions can occur if the environment changes. It went on to examine the evidence for the processes involved in state transitions, pointing to a role for the VAN in monitoring, with the FPCN and DAN more directly active during transition phases (Ellamil et al., 2016; Hasenkamp et al., 2012). It outlined how studying state transitions is more difficult given traditional analyses that take momentary snapshots of experience, and presented several ways in which fMRI data can be best utilised to further our understanding of these processes. For example, studies using dynamic decomposition approaches to understanding state transitions suggest they involve whole-brain reorganisations in low-dimensional space that are mediated by neuromodulatory subcortical inputs (Karapanagiotidis, Vidaurre, et al., 2019; Shine et al., 2018; Shine et al., 2019).

This chapter provides the motivation for the paradigm used in this thesis to investigate ongoing thought. This paradigm utilised:

- MDES to gain a detailed picture of different states along multiple dimensions.
- Two conditions that vary in their need to maintain external task states, so that the role of context in ongoing thought can be modelled appropriately.
- Relatively rare, intermittent target trials that provide a defined moment of external attention from which the emergence of internal states over time can be modelled.

By ensuring these aspects are correctly accounted for, measures of ongoing thought can be related to cognitive measures and fMRI data to give a clearer picture of the neurocognitive systems involved in ongoing thought. The next chapter will elaborate this further, giving a more detailed outline of the paradigm and examining several studies that have already used it to investigate ongoing thought. It will also provide a refresher on the different ways to relate brain activity to experience sampling data to identify the neurocognitive systems engaged during state maintenance and transitions.

Chapter 2 – The Current Thesis

2.1 Introduction

By understanding ongoing thought in terms of a state framework, each moment can be thought of as existing within a state space. The current state can be described as a location in this multidimensional space, defined by its characteristics along dimensions including whether it is internally or externally focused, how detailed it is, whether it is positive or negative emotionally, and so on. A snapshot of experience at any moment will either capture a state that is being maintained, remaining roughly in the same area of state space, or a transition between two states, movement along one or more dimensions. In order to understand the processes that are involved in state transitions and maintenance, it is necessary to attempt to capture as much information as possible about the location of an individual in this state space, and to leverage experimental design to encourage both state maintenance and transitions. This thesis uses MDES to capture the location of individuals along multiple dimensions of experience to estimate their location in state space over the course of a task-based experiment that includes two conditions that vary in their demands. By modelling the relationship between neurocognitive measures either taken separately (trait) or simultaneously (state) and measures of ongoing thought, and including task condition and time since task performance as independent variables, it enables a thorough delineation of the systems involved during state maintenance and transitions. This chapter will first provide a more detailed outline of the paradigm used, showing how each feature was designed to provide clarity to the literature on ongoing thought. It will then go on to explain how trait and state measures of fMRI provide information about the neurocognitive processes involved in ongoing thought. In this section, it will also review a range of studies that have used this paradigm to understand ongoing thought, using them to highlight the ways in which this paradigm can be combined with fMRI.

2.2 The Paradigm

In the previous chapter, it was shown that ongoing thought has varied outcomes and relationships to certain neurocognitive processes in the literature. It was described how these complications largely result from the multidimensional nature of ongoing thought, as well as the need to consider context and dynamics when evaluating the outcomes and neurocognitive basis for specific aspects of ongoing thought. The

paradigm used throughout the current thesis was designed to provide clarity in these discussions of ongoing thought. Along with utilising a state-space approach to understanding ongoing thought, these design properties can be capitalised on to provide clarity on the neurocognitive systems that are engaged during different states and in the transitions between them. The next three paragraphs will start with a reminder of the specific consideration needed when studying ongoing thought, and will then go on to explain in more detail how each design feature helps to resolve it.

2.2.1 Multi-Dimensional Experience Sampling

Ongoing thought has varied outcomes, for example, it can be related to both positive (McMillan, Kaufman, & Singer, 2013) and negative mood (Killingsworth & Gilbert, 2010). This relationship partly depends on the nature of the thoughts: interesting thoughts have been shown to relate to positive mood (M. S. Franklin, Mrazek, et al., 2013), and past-related thoughts are more strongly related to negative mood than future ones (Ruby, Smallwood, Engen, et al., 2013). Specific types of future thinking can reduce anxiety (Jing, Madore, & Schacter, 2016), improve prosociality (Gaesser & Schacter, 2014), and improve mood (McMillan et al., 2013). Different components of thought with different associated neural connectivity have shown opposing relationships to measures of well-being and cognition (H.-T. Wang, D. Bzdok, et al., 2018). These results highlight the importance of understanding the specific nature of ongoing thoughts before it is possible to understand its outcomes and the processes engaged while it is occurring. In terms of state space, this means gaining a picture of where the participant's state is located along multiple dimensions. For this reason, this thesis used a design that included MDES probes asking 13 questions about the nature of a participants' thoughts throughout task performance. These questions were then decomposed using PCA to give a description of participants' thoughts along 4 dimensions: on- to off-task, vague to detailed, words to images, and positive to negative emotional valence. This enabled the neurocognitive systems involved in specific states to be investigated.

2.2.2 Varied Task Context

Even within the same dimension of experience, ongoing thought can have different relationships to neurocognitive processes and opposing outcomes. Forms of off-task thought are a major source of performance errors (Kane et al., 2007;

Smallwood, Fishman, et al., 2007), but can also improve creative problem solving (Baird et al., 2012). These same thoughts have been both positively (Levinson et al., 2012) and negatively related to measures of executive control (McVay & Kane, 2009). These differences are largely driven by context: having large numbers of off-task thoughts during a difficult task causes performance errors (McVay & Kane, 2012a), but allowing these thoughts to emerge during a simple task does not cause these same errors (Konishi et al., 2017). Thinking in terms of states, a difficult task requires the maintenance of external states requiring executive resources, whereas a simple task encourages the maintenance of internal states that are thought to require the support of similar resources (Smallwood, 2013a). The paradigm used in this thesis has two conditions. The 0-back task consists of multiple non-target trials interspersed with target trials that ask the participant to locate a centre shape from two shapes on either side of it. The use of this simple, perceptually-guided decision means that this task does not require continuous monitoring to perform (as the non-targets do not include information that is pertinent to task performance). This encourages internal states to be maintained for longer periods during this task. The 1-back task replaces these targets with trials that require the participant to locate a centre shape from two shapes on either side of the preceding trial. This means that this condition does require continuous monitoring, in case the information from a non-target is needed in the upcoming target trial. This necessitates the maintenance of external states during this condition. This has two benefits: firstly, it causes different states to be maintained, meaning the neurocognitive systems involved in these state can be better identified utilising the increased variance. Most importantly, it allows for the processes involved in maintaining specific states to be separated from those involved in maintaining states across conditions. For example, a process that is engaged more strongly during internal states in the 0-back and external states during the 1-back would represent a mechanism for state maintenance shared across these states that acts to insure task-appropriate states are maintained. A process engaged exclusively during the maintenance of external states irrespective of task context would be more specific to these states. By including these conditions, this thesis can use contrasts that include main effects and interactions with task context to separate systems involved in internal states from those involved in external states, as well as those involved more generally to guide appropriate state maintenance. This will help to resolve specific debates in

the literature, specifically related to whether executive control is needed to maintain internal or just external states (McVay & Kane, 2010; Smallwood, 2010).

2.2.3 Elapsed Time

Lastly, it is useful to separate ongoing thought into processes involved in state maintenance from those involved in transitioning between states (Smallwood, 2013a). Processes involved in maintaining states are comparatively easy to study by utilising tasks that ensure the participant has to maintain specific states in order to perform the task and then probing these processes using fMRI or other measures of cognition. The processes involved in state transitions are poorly understood, although they are known to result from whole-brain reorganisations in low dimensional space (Karapanagiotidis, Vidaurre, et al., 2019; Shine et al., 2019) and engage processes in the FPCN and DAN (Ellamil et al., 2016; Hasenkamp et al., 2012). These processes require specific design features to understand. In this thesis, the paradigm involves a sequence of non-targets trials which require no action by the participant, with less common target trials that require a motor action to choose which side of the screen a specific shape is, or was, located on. This means that during the moment of target trial performance, the specific state of the participant is defined by the requirements of the task. In the 0-back, the participant is encouraged to transition from this perceptually-guided decision-making state towards an internal state during a sequence of irrelevant non-target trials. In the 1-back, the participant is required to maintain an external focused task state during non-targets that may contain task-essential information. By varying the number of non-target trials between each target, this paradigm allows an assessment of whether the length of time since the last task-related action leads to differences in the state of the participant, providing insight into how states change over time. This can also be modelled as an interaction with task condition to understand how the external requirements of the task modulate this relationship.

This paradigm was originally developed with a single thought probe pertaining to task focus (Konishi et al., 2015) and it was shown that, as expected, individuals were more task-focused in the 1-back condition. This paradigm is used in all four experimental chapters of this thesis in two variations: a version that is carried out in three 25-minute blocks over the course of three days in the behavioural laboratory and one that was carried out in four 9-minute runs while undergoing fMRI scanning. Taking

measures over three days and decomposing them using PCA provides the structure of trait-like ongoing thought across participants. It also identifies the degree to which these dimensions of thought are dependent on task context, and provides individual differences in both the types of states that are maintained and context regulation. For example, a participant who engages in high off-task thought in the 0-back and high on-task thought in the 1-back across three days has a trait structure along this dimension that shows effective context regulation of this dimension. This means that this participant is able to engage cognitive processes necessary for this regulation consistently in their ongoing thought. This participant will also do well on tasks that require the same processes as context regulation and show a trait brain architecture that reflects this. By comparing this trait ongoing thought to task measures and resting state fMRI it will enable insight into these processes. Additionally, during fMRI scanning the participant will engage these same processes and activate regions necessary for this aspect of cognition. Using these two approaches therefore provides two ways of probing the cognitive processes engaged during ongoing thought, and provides improved reliability if similar results are found across experimental conditions.

2.3 fMRI as a Measure of Ongoing Thought

fMRI provides an indirect measure of brain activity by measuring where oxygenated blood is used in the brain: the blood-oxygen-level-dependent (BOLD) signal. This activity can be used to understand the processes that are engaged during ongoing thought in two different ways that will be leveraged in this thesis.

2.3.1 Resting State fMRI

Functional connectivity refers to the correlation between BOLD signal in one area of the brain with that in another (Friston, 1994). If there is a high correlation between these signals then the regions are said to show high functional connectivity. This approach can use a defined seed region and a whole-brain search to identify regions that show correlation with the seed (D. V. Smith et al., 2014), or it can use pre-defined regions-of-interest and assess connectivity between these (Marrelec & Fransson, 2011). The usefulness of this approach relies on the fact that functional connectivity measured at rest reflects trait cognitive processing (Cordes et al., 2000), as processing that is carried out more often will result in stronger connectivity over time that is reflected in the brain at rest (Biswal, Zerrin Yetkin, Haughton, & Hyde,

1995). Using an example from a well-studied field, the amygdala (a region involved in processing salience and fear (Blackford, Buckholtz, Avery, & Zald, 2010; LaBar, Gatenby, Gore, LeDoux, & Phelps, 1998; Pessoa & Adolphs, 2010)) shows functional connectivity to the medial pre-frontal cortex (a region involved in top-down cognitive control (Badre & Nee, 2017)). This connectivity has been shown to relate to the ability to regulate emotions, and is deficient in anxiety disorders in which the ineffective management of emotion is a key component (Kim et al., 2011). This highlights the way in which resting state fMRI can be used to understand cognitive processes. Functional connectivity has also been shown to reflect a trait-architecture of the human brain that contains information about an individual's identity, including their ongoing thought (Finn et al., 2015; Gratton et al., 2018), and differences in functional connectivity have been related to a range of cognitive (Rosenberg et al., 2016), personality (Passamonti et al., 2015), experiential (Smallwood et al., 2016), and clinical measures (Hull et al., 2017; Konrad & Eickhoff, 2010; Sheffield & Barch, 2016). This thesis will compare the resting state connectivity of the brain to participants' ongoing thought to understand the processes engaged:

- Chapter 3 will leverage differences in ongoing thought across conditions and over time to understand how the trait architecture of brain systems relates to specific states engaged over three days during task performance. It will attempt to separate these from those that are related to more general aspects of cognition such as the ability to regulate states in line with environmental demands, and those involved in state transitions.

- Chapter 4 will probe measures of functional connectivity within a region identified by its involvement in context regulation in-the-moment to better understand the mechanisms of this phenomenon.

- Chapter 5 will look at relationships between functional connectivity and measures of autistic traits to understand if the trait functional organisation of the cortex mediates psychopathological aspects of ongoing thought.

2.3.2 Task-based fMRI

As opposed to BOLD signal collected at rest, task-based fMRI collects BOLD signal during task performance and looks for relationships between cognitive processes required by the task and brain activity (Friston, Frith, Turner, & Frackowiak,

1995). The logic behind this approach is simple: if a task involves a certain process that is carried out in a certain brain region or network, then the activity in this part of the brain will be higher during this task (Henson, 2007). It often requires a comparison condition, usually a similar task lacking the specific process of interest, but activity can also be compared to a baseline defined by the non-targets of the task (Linden et al., 1999) or rest (Iacoboni et al., 2004). This type of analysis has found recruitment of overlapping regions related to a range of cognitive processes (Gu et al., 2019; Hardwick, Caspers, Eickhoff, & Swinnen, 2018; Rottschy et al., 2012; Van Overwalle, 2009; Worringer et al., 2019; Xu et al., 2020). This thesis will look at brain activity during ongoing thought to better understand the processes involved:

- Chapter 4 assessed brain activity measured 6 seconds prior to a thought probe for relationships to the position of the participant in state space as measured along 4 dimensions of thought (on- to off-task, vague to detailed, words to images, and negative to positive emotional valence), with a primary focus on identifying processes involved in maintaining on- and off-task states, individually, as well as those that are shared across these states.
- Chapter 6 assessed brain activity during task performance to identify neural changes that occurred with the passage of time form a fixed position in state space to better understand state transitions.

2.4 Previous Studies using the Paradigm

The data from the 25-minute laboratory version of this paradigm has been used in several studies that find evidence for four dimensions of thought: task-relatedness, detail, modality, and emotional valence (Konishi et al., 2017; Poerio et al., 2017; Ruby, Smallwood, Engen, et al., 2013; Sormaz et al., 2018; Vatansever et al., 2018). Two of these studies that used the same data as this thesis tested levels of these dimensions across the two conditions and found thoughts to be more detailed, more on-task, and more in the form of images during the 1-back task (Sormaz et al., 2018; Vatansever et al., 2018). A study relating functional connectivity to thought levels in the data used in this thesis found that reduced connectivity between the core of the DMN (comprising the medial prefrontal cortex and posterior cingulate cortex) and a region in the cerebellum was related to more off-task thoughts. Interestingly, increased connectivity between the medial temporal part of the DMN and dorsomedial prefrontal cortex was

also found to be related to more off-task thoughts in general during this paradigm (Poerio et al., 2017). A second study using this data showed that functional connectivity between the FPCN and visual cortex was linked to more detailed thoughts in a way that moderated the link between maintaining task-related detail and ADHD symptoms (Vatansever et al., 2018). This thesis will build on these results by extending the relationships between functional connectivity and ongoing thought to include associations with both the task condition and the time elapsed since a known task-specific state was engaged. This will enable a better delineation of the role of certain systems in ongoing thought, specifying those that are engaged to maintain certain states, those that are engaged to maintain states more generally across conditions, and those that are related to transitions between states. This thesis will also include an analysis that probes the relationships between autistic traits in this neurotypical sample, ongoing thought, and functional connectivity. As well as providing insight into this important disorder, this study leverages the fact that autism is characterised by differences in both ongoing thought in general (Solomon et al., 2008) and flexibility (Sanders, Johnson, Garavan, Gill, & Gallagher, 2008) to better understand the mechanisms of state maintenance that may be lacking in this population.

Several studies have asked participants to perform the paradigm used in this thesis while undergoing fMRI scanning, only one of which has included thought probes to understand links between ongoing thought and neural activity. The first of these found that a range of regions in the DMN were more active while participants were likely to be in an internal state compared to an external one. Specifically, they were more active during non-targets in the easy 0-back and targets during the memory-guided 1-back than non-targets in the 1-back and targets in the perceptually-guided 0-back (Konishi et al., 2015). A more recent study using an adapted form of this task replicated the result that the DMN is active during memory-guided decision-making (targets during the 1-back) and found that this activation is stronger when the decisions are based on more complex stimuli (C. Murphy et al., 2018). By further adapting the paradigm to include identity as well as location judgements, they showed that this DMN recruitment during memory-guided decision making was independent of the nature of the decision (C. Murphy, Wang, et al., 2019). Lastly, a study using the identical paradigm to the one used in this thesis (including MDES probes) found that information about the levels of detail in participants' thoughts during the 1-back could

be decoded within the DMN, whereas information about off-task thought in the same task could be decoded in regions including the DAN (Sormaz et al., 2018). This thesis will build on these studies in several ways. Firstly, it will use a larger cohort of participants to better understand the processes involved in ongoing thought. This task-based fMRI analysis will be used to identify regions supporting external states, internal states, and those that are shared between these states. A further adaptation of this analysis will be performed that models time since last task event to understand how brain states change over time and how this relates to changes in state transitions measured using experience sampling. It will also contextualise these changes using previous research about large-scale functional hierarchies of brain organisation (Margulies et al., 2016) to understand how the brain moves through state space and whether this space is rooted in the intrinsic architecture of the brain.

2.5 Aims of the Current Thesis

This section has provided an overview of the motivation for using this specific paradigm to understand ongoing thought and the neurocognitive processes involved in state maintenance and transitions. It has explained how previous research has already used this approach to make important discoveries about ongoing thought, and has outlined how this thesis will build on these studies. Finally, it is important to detail the analyses performed in these chapters more specifically, further emphasising what they hope to understand about ongoing thought using this paradigm. The experimental chapters of this thesis are as follows:

- Chapter 3: In this chapter, the 25-minute version of the MDES paradigm will be used over 3 days to capture the trait-like structure of ongoing thought and how participants engage in it across the two conditions. An analysis will be performed that models relationships between the functional connectivity from 4 seeds: the DAN, the VAN, the FPCN, and the DMN, all networks that have been linked to ongoing thought. This analysis will examine the relationship between cognition as represented by this connectivity as well as by 4 measures from tasks (creativity, fluid intelligence, task-switching, and inhibition) and ongoing thought. By modelling both the time elapsed since a known position in state space and the task context, it will provide insight into the role of these 8

cognitive processes in maintaining specific states, maintaining states more generally in line with external context, and state transitions.

- Chapter 4: The task-based fMRI version (four 9-minute blocks) of this task will be used to understand which regions of the brain are active during specific states and which are involved in maintaining states in line with the demands of the task. These regions will provide targets for more specific functional connectivity analyses (using the 25-minute version of the paradigm) to further investigate which processes are involved in maintaining specific states and which help to enable cognition to flexibly vary in line with the needs of the environment.

- Chapter 5: The 25-minute version of the paradigm will be used to assess relationships between specific states and autistic traits in a neurotypical population. These traits will also be related to measures of brain structure and function to better understand the neural basis for these traits, as well as to use autism as a disease model to understand processes involved in state maintenance that may be different in these individuals.

- Chapter 6: The 4x9-minute fMRI version of this task will be used in a model that assesses how brain activity changes over time from a fixed task-specific state. These changes will be related to defined functional hierarchies of brain organisation to examine whether state transitions following task performance can be understood as movement in a state space that is rooted in the intrinsic architecture of the brain. These changes will also be linked to measures of experience obtained using MDES.

As a whole, this thesis aims to help better understand the neurocognitive systems that are engaged during specific states, and in the transitions between them.

Chapter 3 – The ebb and flow of attention: Between-subject variation in intrinsic connectivity and cognition associated with the dynamics of ongoing experience

This chapter is adapted from: Turnbull, A., Wang, H. T., Schooler, J. W., Jefferies, E., Margulies, D. S., & Smallwood, J. (2019). The ebb and flow of attention: Between-subject variation in intrinsic connectivity and cognition associated with the dynamics of ongoing experience. *NeuroImage, 185*, 286-299.

3.1 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 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.

3.2 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. 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; H.-T. Wang, G. Poerio, et al., 2018), some of which may reflect patterns of ongoing thought (Christoff et al., 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; Villena-Gonzalez et al., 2018). 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 et al., 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 (S. M. Smith et al., 2015) and psychiatric conditions (J. 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 et al., 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 et al., 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 cognitive 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 et al., 2016; Golchert et al., 2017; Hasenkamp et al., 2012; Kucyi, 2017; Smallwood et al., 2016). For example, the dorsal attention network involves regions of lateral parietal, occipital, and frontal cortex (Michael D 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 (Michael D 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 et al., 2008), is recruited across task domains whenever cognitive demands increase (Klingberg et al., 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; R. Nathan 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; R Nathan Spreng & Grady, 2010). This network entails posterior and anterior regions of medial frontal and cingulate cortex (Greicius et al., 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 et al., 2015; C. Murphy et al., 2018; Vatansever et al., 2017). These states of memory-guided thought include periods of off-task thought (Christoff et al., 2009), imagining the future (Østby et al., 2012; R Nathan 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).

3.2.1 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, et al., 2008; Smallwood et al., 2004), and individuals with poor attentional control (M. S. Franklin et al., 2017; Seli, Smallwood, et al., 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, 2009, 2012b; Mrazek et al., 2013). On the other hand, off-task experiences have been linked to better creativity (Baird et al., 2012; H.-T. Wang, G. Poerio, et al., 2018), social problem solving (Ruby, Smallwood, Sackur, et al., 2013), and planning (Baird et al., 2011; McMillan et al., 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 (M. D. Fox, Snyder, Barch, Gusnard, & Raichle, 2005), its associations with worse task performance (Smallwood, Tipper, et al., 2013; Weissman et al., 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 (H.-T. Wang, G. Poerio, 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, 2013b). 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.

3.3 Methods

3.3.1 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.

3.3.2 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.

3.3.3 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
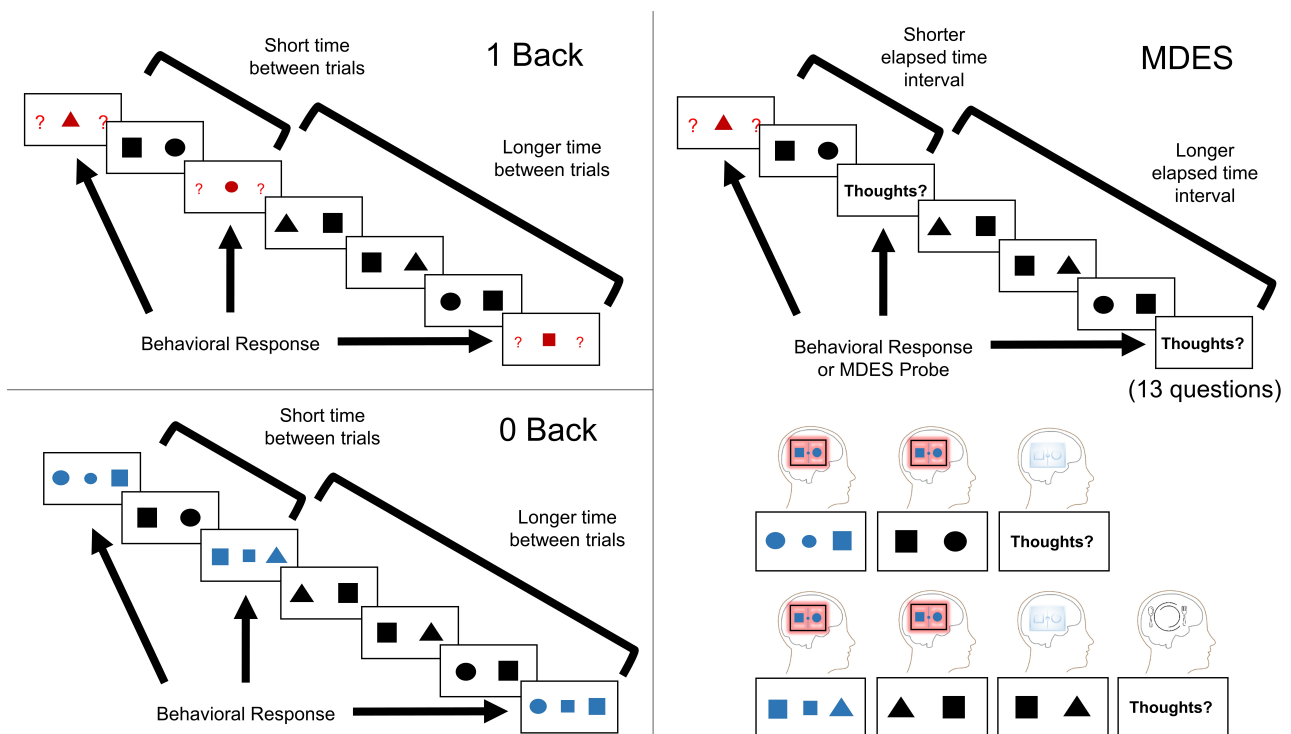
Figure 1. Ongoing thought was measured during blocks of alternating 1-back (top left) and 0-back (bottom left) tasks. During target trials individuals had to state the location of the centre shape in either the on-screen trial (0-back) or the preceding trial (1-back). The condition was denoted by the 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.

had to maintain the visuo-spatial array in 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 et al., 2017; Medea et al., 2016; Ruby, Smallwood, Engen, et al., 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.

3.3.4 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.

3.3.4.1 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.

3.3.4.2 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.

3.3.4.3 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.

3.3.4.4 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.

3.3.5 Resting State fMRI

3.3.5.1 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.

3.3.6.2 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.

3.3.7 Data Analysis

3.3.7.1 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.

3.3.7.2 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 et al., 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).

3.4 Results

3.4.1 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.
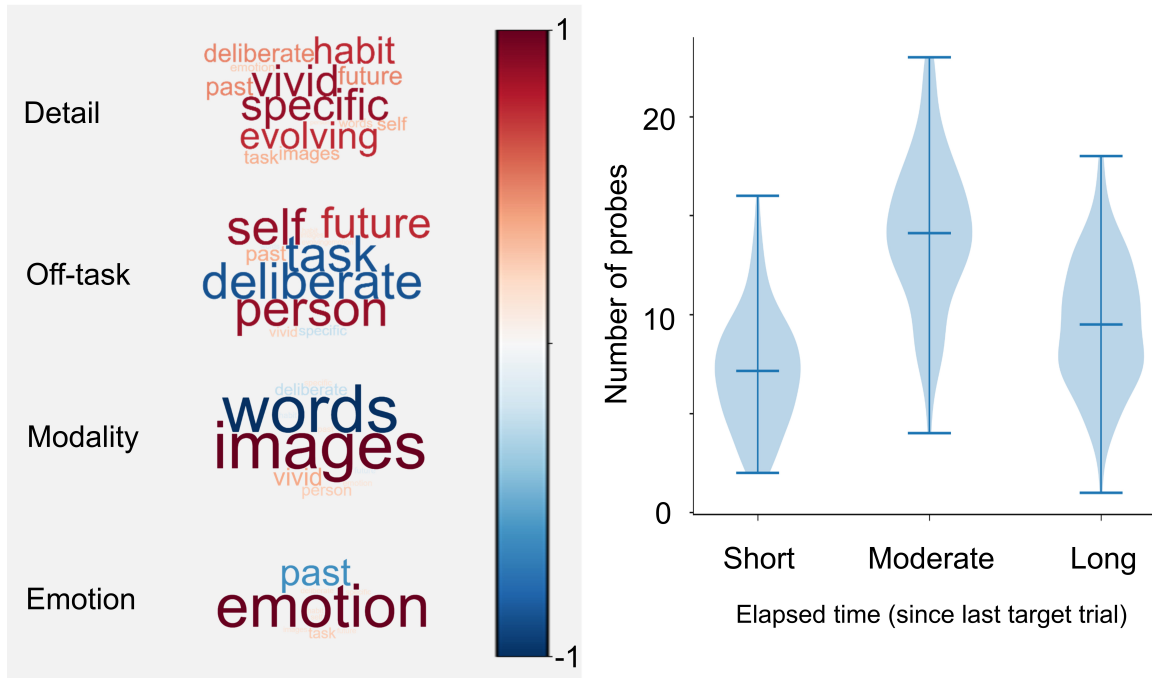
Figure 2. Experience sampling probes revealed four components of thought. Principal Components Analysis applied to the 13 experience sampling questions resulted in four principle components of thought. The wordclouds on the left describe the loadings of each item for these components, with the size representing 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.
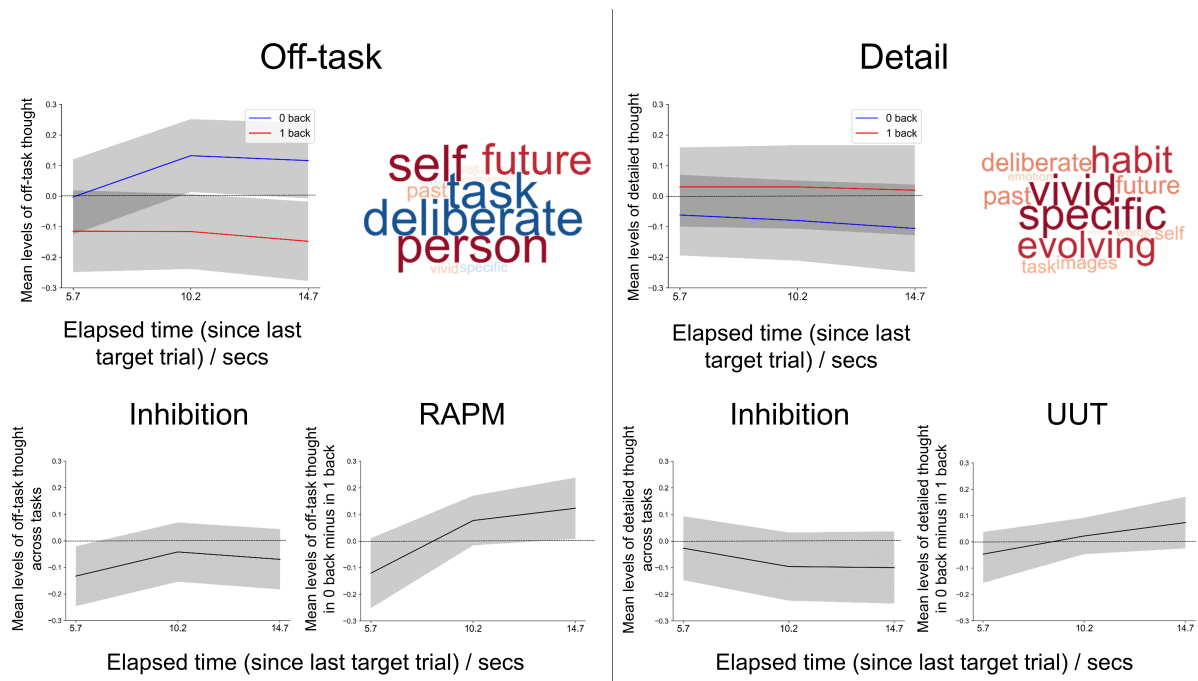
Figure 3. Relationship between elapsed time, task, and components of cognition (creativity, fluid intelligence, and flexibility) and patterns of ongoing thought (n = 157). Off-task thought showed greater increases with time under non-demanding conditions dependent on fluid intelligence. Detailed thought 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.

3.4.2 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 (Thomas 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/).

3.4.3 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.

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

High/low = median split by dorsal attention network (DAN) connectivity to lateral occipital cortex

High/low = median split by ventral attention network (VAN) connectivity to motor cortices

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.

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.

3.4.4 Fronto-parietal and Default Mode Networks
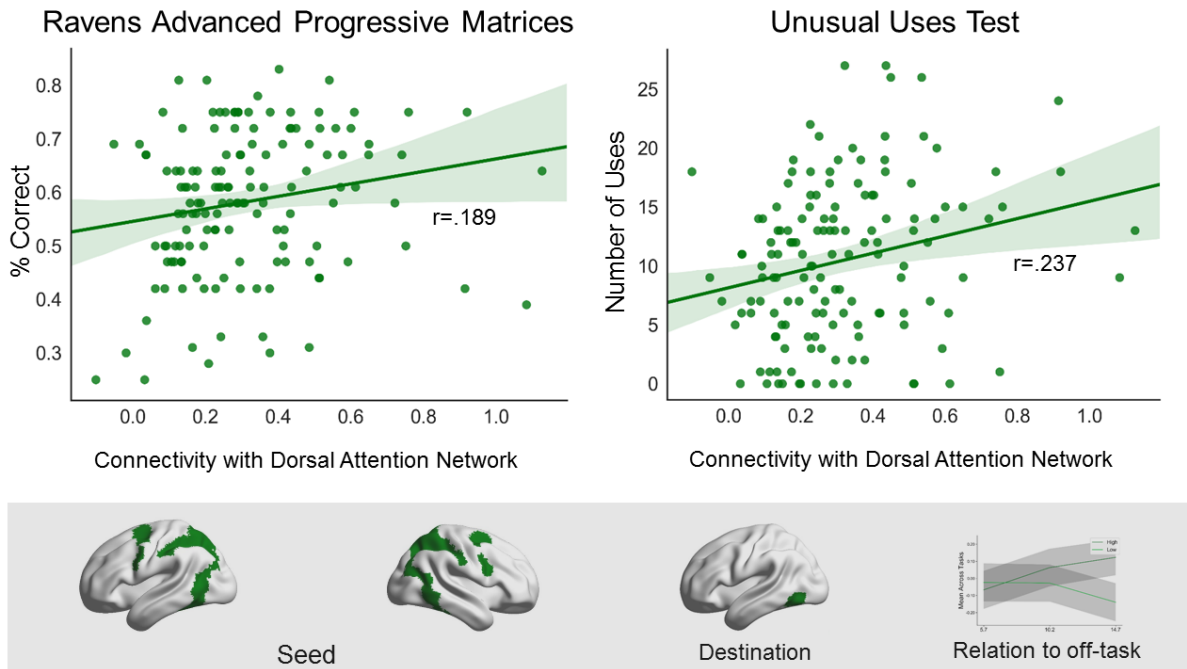
Figure 5. Correlation analysis identified significant relationships between the connectivity of the left lateral occipital cortex and dorsal attention network, identified through an analysis of patterns of ongoing thought, and measures of fluid intelligence and creativity (n=141). The connectivity of 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).
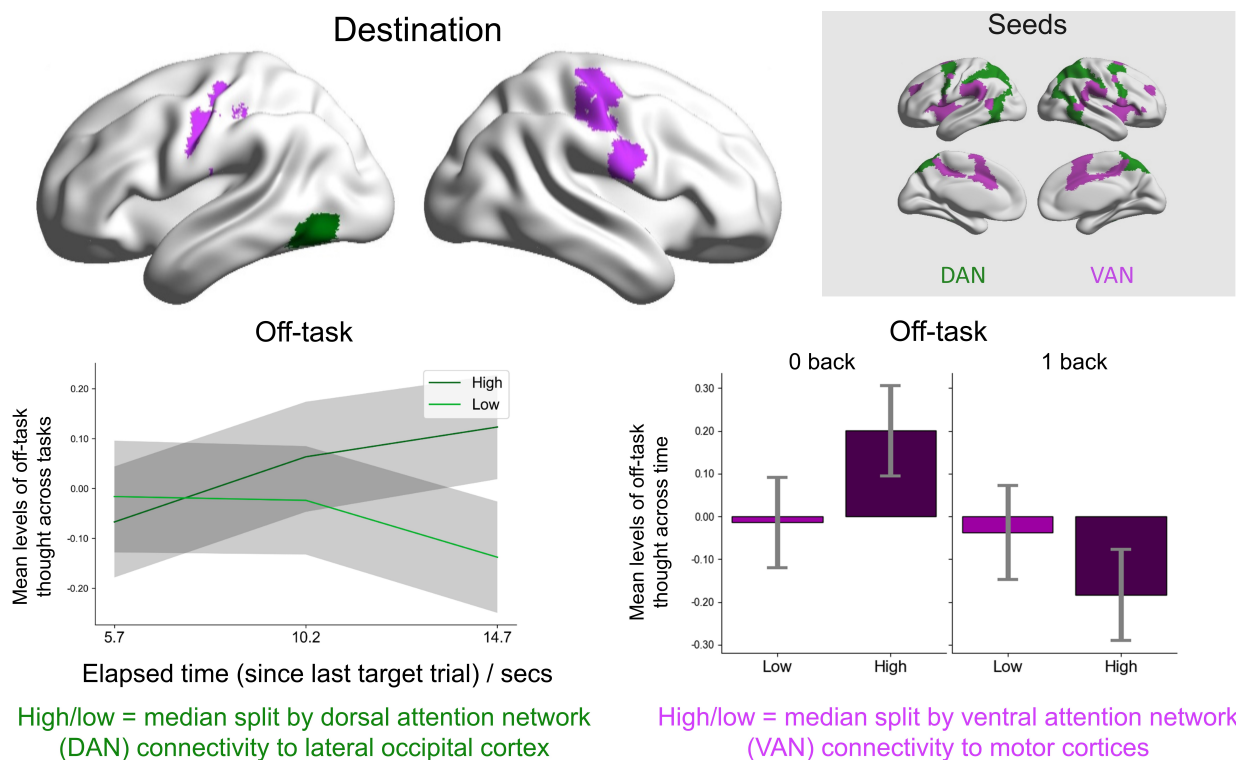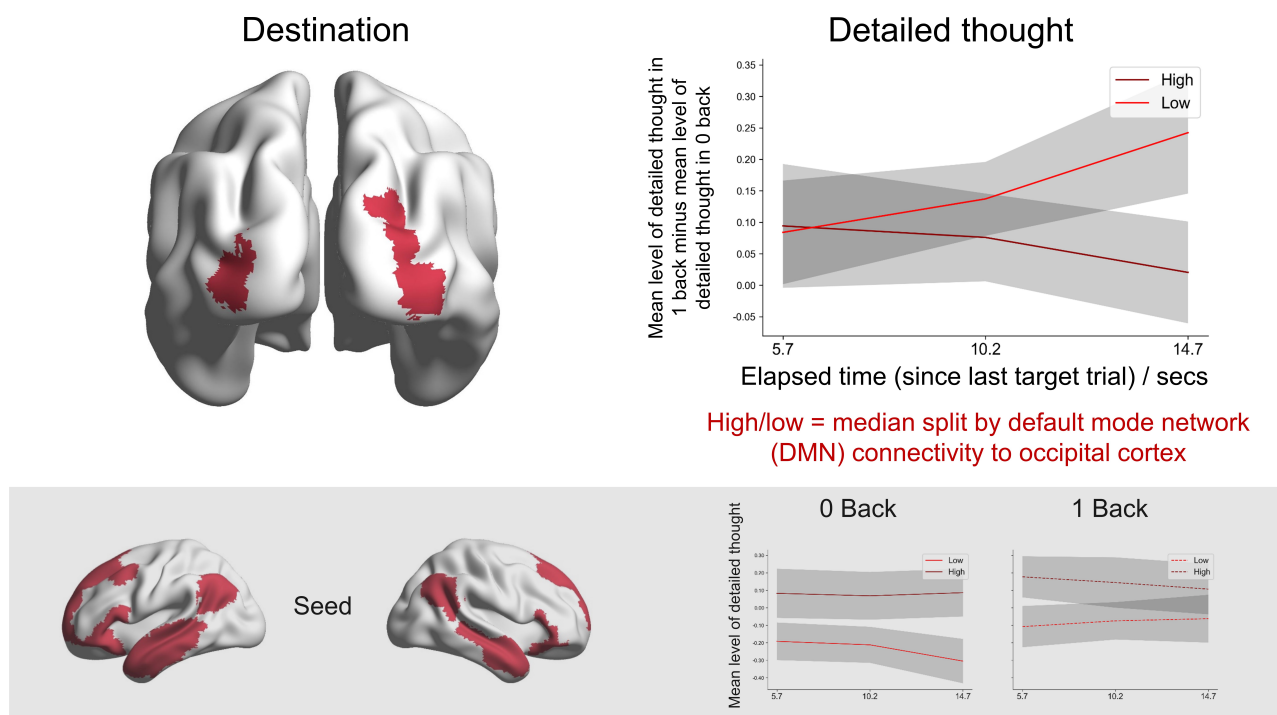

Figure 6. Group level regression using detailed PCA scores as regressors of interest revealed significant clusters for the default mode network (n=141). Connectivity between the default mode network and two significant clusters in bilateral visual cortices were related to a pattern of increasingly detailed 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 et al., 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 (Thomas 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.
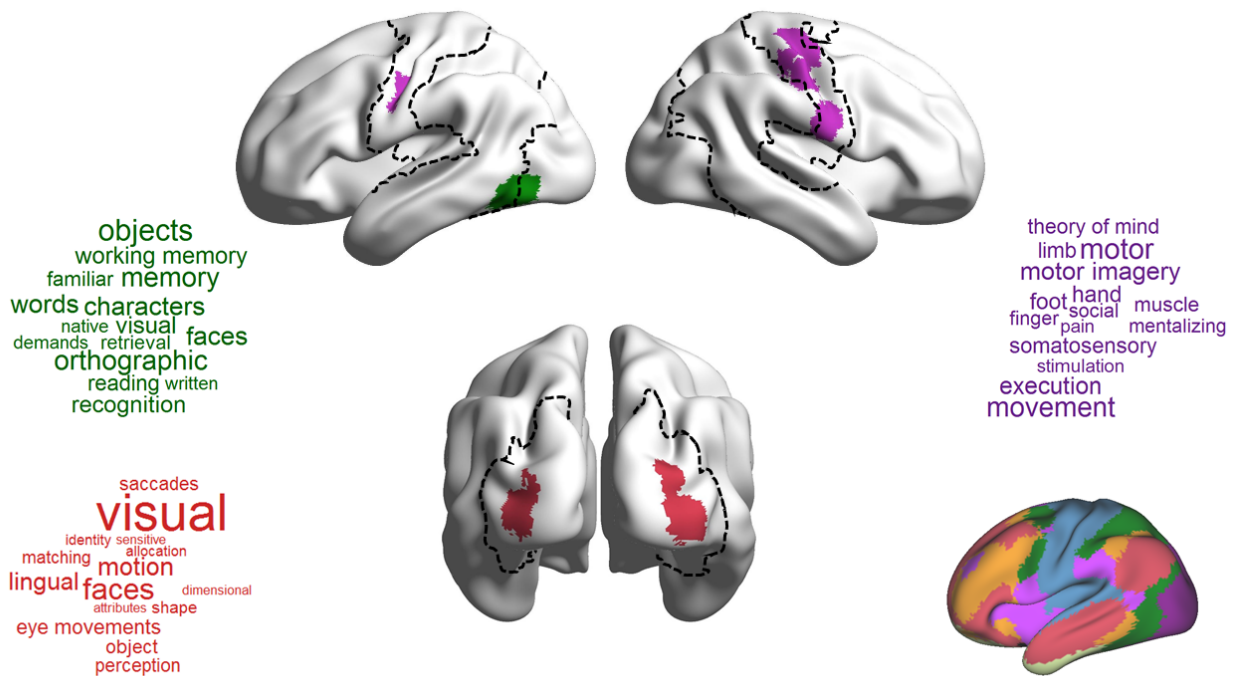
Figure 7. All significant clusters from the group level resting state analysis fall in primary sensory regions (n=141). Dotted lines show the outlines of the visual and sensorimotor networks as defined by Yeo and Krienen et al. (2011). The dorsal attention result occurred at the border of visual and 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.

3.5 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 (M. S. 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; M. 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, Beach, 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 (R Nathan 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; C. 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 et al., 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, 2013b). 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, 2013a). 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 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; S. M. 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, 2012b; 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 (J. W. 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 individual's 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 (C. 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.

3.6 Conclusion

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.

Chapter 4 – Left dorsolateral prefontal cortex supports context-dependent prioritisation of off-task thought

This chapter is adapted from: Turnbull, A., Wang, H. T., Murphy, C., Ho, N. S. P., Wang, X., Sormaz, M., ... & Smallwood, J. (2019). Left dorsolateral prefrontal cortex supports context-dependent prioritisation of off-task thought. *Nature communications*, *10*(1), 1-10.

4.1 Abstract

When environments lack compelling goals, humans often let their minds wander to thoughts with greater personal relevance; however, we currently do not understand how this context-dependent prioritization process operates. Dorsolateral prefrontal cortex (DLPFC) maintains goal representations in a context-dependent manner. Here, we show this region is involved in prioritising off-task thought in an analogous way. In a whole brain analysis we established that neural activity in DLPFC is high both when 'on-task' under demanding conditions and 'off-task' in a non-demanding task. Furthermore, individuals who increase off-task thought when external demands decrease, show lower correlation between neural signals linked to external tasks and lateral regions of the DMN within DLPFC, as well as less cortical grey matter in regions sensitive to these external task relevant signals. We conclude humans prioritize daydreaming when environmental demands decrease by aligning cognition with their personal goals using DLPFC.

4.2 Introduction

Humans often use periods of low environmental demands to consider topics with greater relevance than events in the here-and-now (O'Callaghan et al., 2015; Smallwood, 2013b). Studies have linked the capacity to self-generate trains of thought that are decoupled from external input with beneficial psychological features including delaying gratification (Smallwood, Ruby, & Singer, 2013), creative problem solving (Baird et al., 2012; Smeekens & Kane, 2016; H.-T. Wang, G. Poerio, et al., 2018), and in refining personal goals (Medea et al., 2016). Other studies, particularly those that measure ongoing experience in externally demanding task contexts, have shown that off-task self-generated thought has been linked to worse executive control and can be a cause of poor performance (McVay & Kane, 2009, 2012a; Mrazek et al., 2012;

Robison & Unsworth, 2015; Unsworth & Robison, 2016). It has been argued that this apparent contradiction could be reconciled by assuming a general role of control processes that maximises the fit between patterns of ongoing experience and the demands imposed by the external environment (Smallwood, 2013a). This view, known as the context regulation hypothesis, predicts a common control process underpins both the act of reducing off-task thought when external demands are high, and increasing thoughts about personally relevant information when the environment lacks a compelling goal.

The context regulation hypothesis is hard to test behaviourally because studies have shown that periods of off-task experience interfere with task performance (McVay & Kane, 2009; Smallwood, Beach, et al., 2008), suggesting that their occurrence can bias task-based estimates of an individual's working memory capacity (Mrazek et al., 2012; Unsworth & Robison, 2016). Accordingly, this study addresses this gap in the literature by using covert measures of cognition derived from functional magnetic resonance imaging (fMRI) to understand how individuals prioritise off-task experience when task demands are low. Based on prior neuroimaging studies, the process of goal-motivated prioritization may depend upon regions that make up the ventral attention, or salience, network (Corbetta et al., 2008). This network includes regions of dorsolateral frontal (Brodmann Area, BA, 9/46) and parietal cortex (BA 40), the anterior cingulate (BA 24 and 32) as well as structures including the anterior insula. This network is important in influencing the maintenance of tasks sets (Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008) across a broad range of contexts including listening to music (Sridharan, Levitin, & Menon, 2008), pain (Wiech et al., 2010), and states of empathy/theory of mind (Kanske, Böckler, Trautwein, & Singer, 2015). The wide range of contexts within which the ventral attention network influences neural dynamics and cognition, suggests that it could be important in the process of context regulation. Consistent with this perspective, a previous study from our laboratory found that individual variation in the connectivity of the ventral attention network was related to population variation in the context-dependent regulation of off-task thought (Adam Turnbull et al., 2019). In two experiments combining measures of experience with neural function, we test the hypothesis that the ability to prioritise personally-relevant thoughts during periods of low external demand depends on a domain-general neuro-cognitive process that helps aligns cognition with the most currently relevant goal

(Smallwood, 2013a). In particular, we examine (a) whether a common neural region is involved in both the prioritisation of off-task thought when task demands are low and the facilitation of on-task thought when environmental demands are increased, and (b) the neural mechanisms that help individuals focus attention on personally relevant information under these circumstances.

4.3 Results

4.3.1 Identification of an Off-task Thought Component

To create conditions varying the requirement for external attention, we used a paradigm which alternated between a higher demand condition in which task-relevant information is maintained in working memory (1-back) and a condition with no equivalent requirement (0-back, Figure 1). While performing these tasks, participants intermittently provided descriptions of their ongoing thoughts using Multi Dimensional Experience Sampling (MDES). This entails the participants describing their experience along a variety of questions including whether they were thinking about the task, focused on themselves, or on future or past events (see Table S1 for the full set of questions). In this paradigm we routinely observe that participants engage in more off-task personally relevant thoughts in the easier 0-back paradigm (Konishi et al., 2015; Sormaz et al., 2018). In this study there were 24 MDES probes in the scanning experiment, yielding a total of 1438 observations for Experiment 1, and 30.7 on average in each session in the behavioural laboratory, yielding a total of 4482 observations in Experiment 2. We applied principal component analysis separately to the MDES data recorded in each dataset, in both cases identifying an off-task dimension (low component loadings on task, high loadings on episodic and social content). These components are presented as wordclouds in Figure 1 and are highly similar across datasets ($r(11)=.882$, $p<.001$). Individual variation in off-task thinking was correlated across settings (0-back $r=.475$, $p=.002$; 1-back $r=.389$, $p=.014$) and more common in the 0-back task in both experiments (scanner: $t(59)=5.997$, $p<.001$, lab: $t(145)=7.120$, $p<.001$). In Experiment 1, neural data was acquired while participants performed this task and greater activity in superior parietal, sensorimotor, and mid-cingulate cortex was observed during 1-back blocks. Activity was greater in medial prefrontal, cingulate, and temporal cortex in 0-back blocks (Figure 1 and Table S2), replicating previous studies (Konishi et al., 2015; Mason et al., 2007).
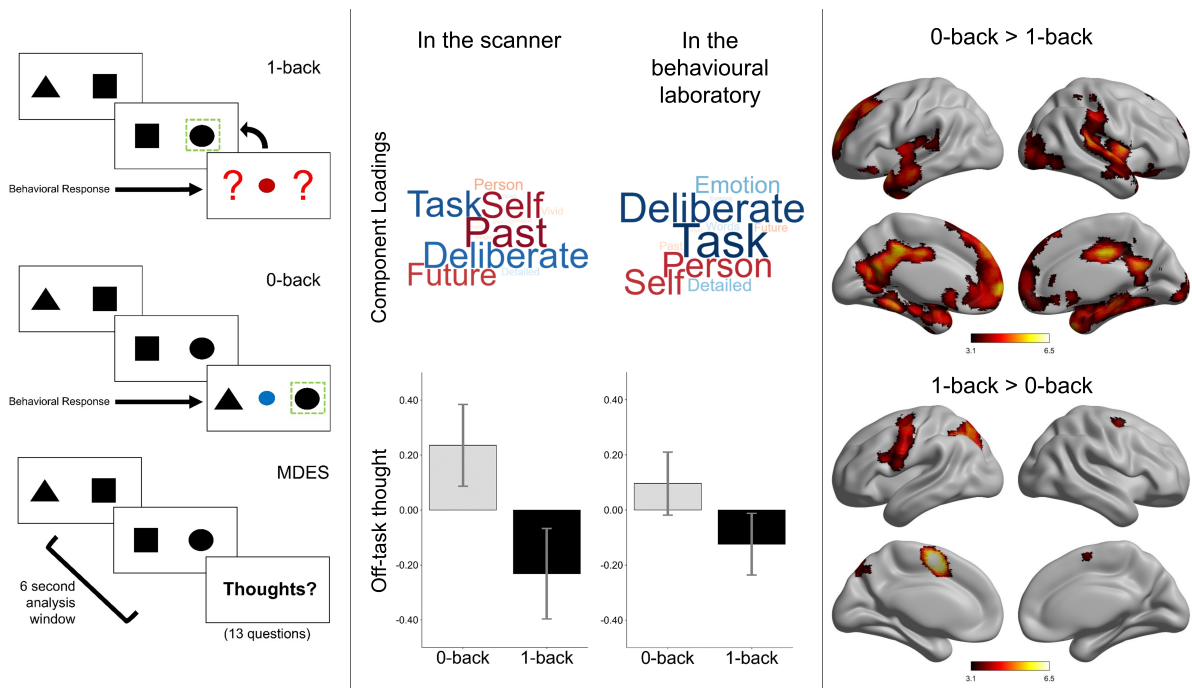
Figure 1. 0-back and 1-back tasks vary in their need for external attention in the scanner and the laboratory. Participants performed alternating blocks of two tasks (left). In the 0-back task, off-task thinking was increased (middle) in both the laboratory and scanner. The application of principal component analysis to MDES data identifies dimensions of thought by grouping questions that capture shared variance. One component identified in this manner captures a dimension that varies from a focus on the task to thoughts about the self and other and with an episodic focus, corresponding to one common definition of off-task mind-wandering (Smallwood & Schooler, 2015). The loadings on this component are presented in the form of wordclouds. Words in a larger font indicates items with a greater loading on the dimension and the colour describes the direction of this loading (red: positive, blue: negative). The average score for this off-task dimension of thought in each task is shown in the bar graphs in which the error bars indicate the 95% confidence intervals of the mean. Contrasts comparing neural activity across these conditions showed increased activity in default mode network regions during the 0-back, and left lateralised frontal and parietal regions during the 1-back (right). Task maps are corrected with a cluster forming threshold of Z>3.1, at a family-wise error rate of p<.05.

4.3.2 fMRI Analysis to Find Regions Related to Context Regulation

Having established patterns of off-task thinking using MDES, we next examined the neural associations with these patterns of thinking. In particular, we focused on how individuals prioritise this information when external demands are low, and how they prioritise on-task thinking when task demands are increased. We examined associations between momentary changes in off-task thinking and associated patterns of neural activity in both tasks (see Methods). If a neural region represents the prioritisation of cognition in line with external demands (Smallwood, 2013a), stronger neural responses should occur in this region when focusing on (a) task-relevant information in a situation of increased task demand, and (b) personally-relevant

information in situations with reduced task demands. We performed a whole-brain fMRI analysis to see whether any regions of the brain had this neural profile. We found that greater off-task thinking in the 0-back, and greater on-task in the 1-back task were associated with increased neural activity within left dorsolateral prefrontal cortex (DLPFC) (Figure 2). To understand how our findings related to cognitive functions most commonly associated with these areas by prior studies in the literature, we performed a meta-analytic decoding using Neurosynth (Yarkoni et al., 2011). This analysis identifies terms in the literature most commonly associated with specific brain regions. Meta-analytic decoding of left DLPFC region identified through our analysis highlighted the term "executive" as most appropriate, indicative of a role for the region in cognitive control. To understand how this region fit into the broader neural architecture, we performed a seed-based functional connectivity analysis (see Supplementary Figure 4). Intrinsic functional connectivity was observed with anterior insula, mid-cingulate cortex, anterior temporal parietal junction, regions that form the ventral attention network (VAN), which has been shown to play a role in task-set maintenance (Dosenbach et al., 2008), attentional re-orienting, and contextual cueing (Vossel, Geng, & Fink, 2014).

We also found that bilateral clusters in the intraparietal sulcus (Figure 2) were linked to more on-task thought across both tasks. Meta-analytic decoding revealed general task properties (e.g., "goal", "attention", "switching", "task") and more specific associations with external numeric tasks (e.g., "calculation"). Functional connectivity was observed with lateral frontal, mid-cingulate and temporo-parietal cortex, corresponding to the dorsal attention network (DAN). This network shows activity during spatial-orienting of visual attention and exerts top-down control over visual areas (Vossel et al., 2014).
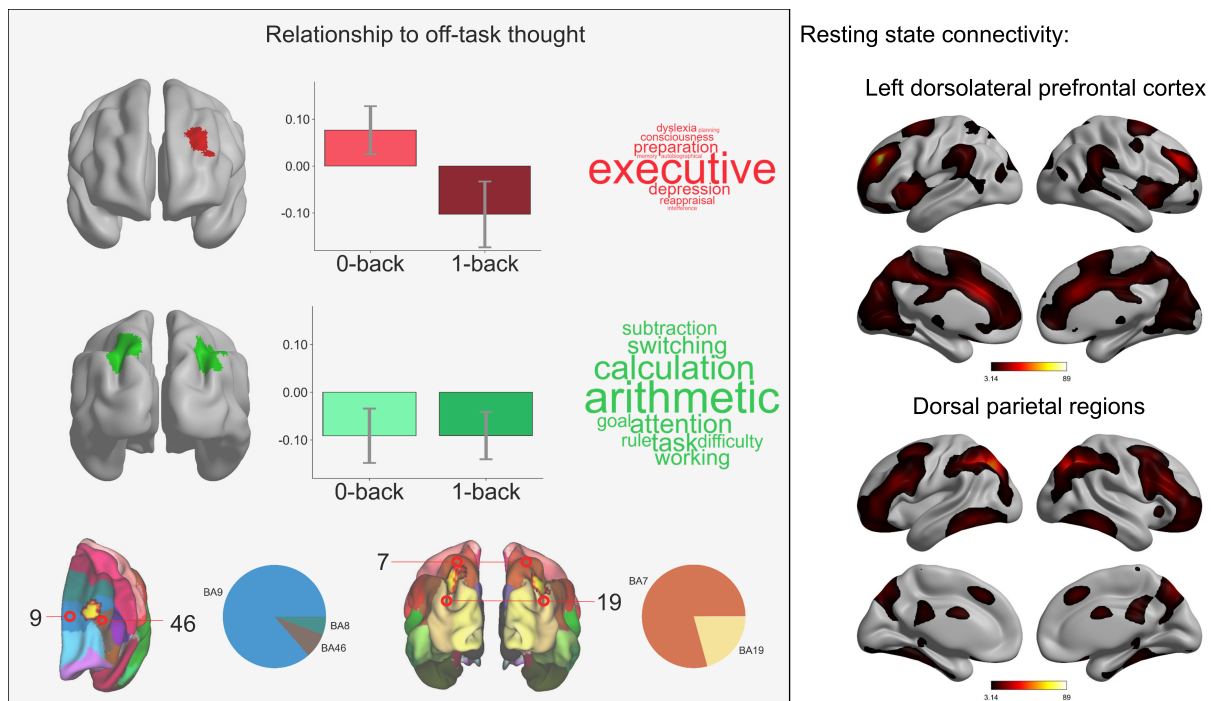
Figure 2. Establishing regions supporting on-task experience and those involved in the regulation of ongoing thought in line with the demands of the external environment. A region of dorsolateral prefrontal cortex (BA8, 9, and 46) was related to off-task thought during the 0-back and on-task thought during the 1-back (top and bottom left). Bilateral parietal regions (BA7 and 19) were related to on-task thought irrespective of task demands (middle left, centre bottom). The pie charts indicate the overlap of the regions identified by our analysis with Brodmann areas to enable a clearer understanding of their anatomical location. These regions show different patterns of resting-state functional connectivity (right). Wordclouds represent associations from meta-analytic decoding (Yarkoni et al., 2011). Statistical thresholds are identical to those in Figure 1.

Experiment 1 establishes two aspects of the neural correlates of off-task thinking across situations with varying environmental demands. First, neural activity in left DLPFC is correlated with being on-task when task demands are higher, and off-task thoughts when demands are lower. This suggests that within left DLPFC periods of personally-relevant concerns under situations of lower external demand share a similar neural correlate to periods of task-focused thought in a more demanding task context. Second, dorsal parietal cortex was associated with being on-task in both conditions, suggesting a more specialised role in external task-relevant processes in regions of the intraparietal sulcus, and a more abstract role in DLPFC that reflects the relationship between ongoing cognition and the level of external demands.

4.3.3 Network Interactions within DLPFC Relate to Off-task Thought

Experiment 1 identifies left DLPFC as showing a common neural profile whenever patterns of ongoing cognition match the demands of the environment.

Studies in humans and monkeys suggest DLPFC monitors information in working memory (de la Vega, Yarkoni, Wager, & Banich, 2017; Petrides, 2005) to form a zone of contextual control important for influencing information entering working memory (Badre & Nee, 2017; de la Vega et al., 2017). Contemporary accounts of ongoing thought argue these experiences require a process of functional decoupling of neural signals related to self-generated information from signals which directly reflect environmental input (Smallwood, 2013a). Extrapolating from these accounts, we hypothesised that context-dependent variation in the association with off-task thought observed in our prior analysis occurs because of how neural signals related to the external task (i.e. posterior elements of the DAN) are processed in left DLPFC. In Experiment 2, we analysed resting-state and structural MRI data from 146 individuals who completed the same task in the behavioural laboratory, seeking evidence that neural processing within the left DLPFC is related to an individual's propensity for engaging in off-task thought when task demands are reduced. Unlike Experiment 1, this analysis examines off-task thinking from the perspective of a trait (see: (McVay & Kane, 2009, 2012b; Mrazek et al., 2012; Smallwood et al., 2016; Smallwood, Tipper, et al., 2013) for prior examples of such an approach). Accordingly, sessions in Experiment 2 took place across three separate days to maximise the chances that our MDES captured a reasonably consistent description of the patterns of experience of each individual.

The pattern of association between activity in DLPFC and patterns of on-task/off-task thought observed in Experiment 1 could indicate that neural signals that reflect both task-related and self-generated information are processed within this region of cortex. To test this possibility in Experiment 2 we performed an analysis to determine (a) whether neural signals arising from other regions of cortex are observed in the DLPFC and (b) if the interaction between these signals explained population variation in context regulation. Following Leech and colleagues (Leech, Braga, & Sharp, 2012), we began our analysis by identifying how the timeseries of 17 well-established networks (Thomas Yeo et al., 2011) are represented in left DLPFC, parcellating this region into partially overlapping sub-regions or "echoes" (Leech et al., 2012) corresponding to each network (see Methods). In the context of our experiment, these correspond to aspects of the left DLPFC in which the observed neural signals within our region of interest are correlated with signals arising from other regions of

cortex. Next we produced a matrix of network interactions within DLPFC, which describes how correlated each of these signals was for each individual, allowing us to test how the functional coupling of signals from different networks predicts experience in the lab. Finally, this matrix was analysed to examine if they predicted individual variation in patterns of off-task thought recorded outside the scanner. We hypothesised that decoupling of signals related to external processing based on Experiment 1 (i.e. posterior regions of the DAN) should be linked to greater off-task thought in the 0-back task. Consistent with expectations based on Experiment 1, more off-task thoughts in the 0-back task was related to lower correlation/more negative correlation between Network 5, corresponding to posterior aspects of the DAN, and Network 17, lateral regions of the Default Mode Network (F(1,135)=12.794, p=.0005, see Figure 3). No similar relationship was observed for off-task thought in 1-back blocks.
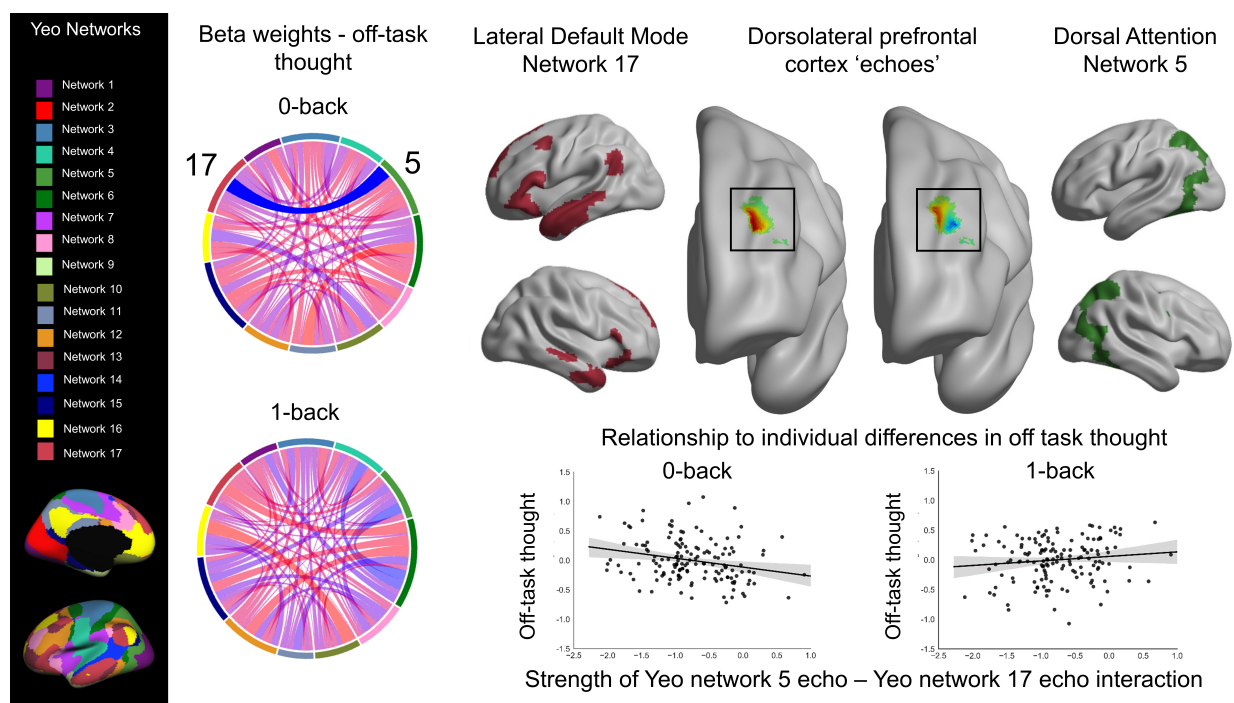
Figure 3. Segregation between echoes of the dorsal attention network and lateral temporal elements of the DMN relate to off-task thoughts in the 0-back condition. Analysis revealed a significant relationship between the correlation of Network 5 and 17 within left DLPFC and off-task thoughts during the 0-back. Chord diagrams represent beta-weights describing the relationship between the strength of pairs of network interactions and reports of thoughts in the 0-back and 1-back tasks. The significant relationship is highlighted (opaque). A key for the networks from Yeo, Krienen and colleagues (Thomas Yeo et al., 2011) is shown on the left, and the chord diagram colours correspond to these. A full description of these networks can be found in Supplementary Figure 8.

4.3.4 Cortical Thickness within DLPFC Relates to Off-task Thought

Our final analysis examined whether individual differences in a more stable neural trait was also related to elevations in off-task thought in the 0-back task by examining experiential associations with the grey-matter structure of the left DLPFC. Our functional analysis indicated signals arising from DAN had a complex topographic pattern within DLPFC, with positive coupling within a dorsal region (BA 9) and negative coupling in a ventral region (BA 46, Figure 4). This separated the region along the border of a sulcus, with the more dorsal region coupled positively to signals related to the task, and the more ventral portion related negatively to the same signals. We hypothesised that if these regions play an important functional role in how individuals focus on self-generated information, then increasing off-task thinking in the 0-back task should be linked to relatively less cortical thickness in regions of left DLPFC sensitive to signals from the DAN. Consistent with this view, relative reduced cortical thickness in dorsal relative to ventral regions was associated with greater off-task thoughts in less demanding conditions ($F_{(2,136)}$ = 3.303, p=.040; Figure 4 and Methods).

4.3.5 Selectivity of the left DLPFC to Off-task Thought

To address the selectivity of the association between neural process in the DLPFC and on-task thought, we performed a number of post hoc analyses. First, using the data we collected in Experiment 1 we extracted the relationship between brain activity in the same area of DLPFC and the other components of thought (Detail, Modality, and Emotion) to see if this region played a role in task-dependent regulation of these. We subtracted the relationship to each component in the 0-back from that in the 1-back, and used the effect seen for off-task thought in Experiment 1 (Cohen's d=0.48) to define the size of the effect we were interested in. We performed equivalence tests (Lakens, 2017) to see if the relationship between the task and thoughts for any other component could be dismissed as null. These were all significant (Detail: $t_{(59)}$=1.978, p=.026; Modality: $t_{(59)}$=2.614, p=.006; Emotion: $t_{(59)}$=3.300, p=.001), suggesting these effects are equivalent to zero and can be rejected as null effects (see Supplementary Figure 5). We were significantly powered to perform this analysis (recommended n=38, effect size Cohen's d=0.48, alpha=.05, power=80%, TOST effect size calculation according to (Lakens, 2017))). This analysis

indicates that task relevant differences in the association with experience were only significant within the left DLFPC for the off-task component of our MDES data. We also performed an equivalence analysis that examined how unique the associations are between cortex-wide signals and patterns of experience within left DLPFC that was observed in Experiment 2 (see Supplementary Table 3). We were significantly powered to perform this analysis (recommended n=97, effect size r=0.2942, alpha=.05, power=80%, TOST effect size calculation). In brief, this found that no other pattern of experience could be predicted based on interactions between the same pair of networks (posterior DAN and lateral DMN) assuming we were looking for an effect of a statistically equivalent size to our significant finding. Moreover, of all the other network pairs included in our analyses all but one association with experience failed to pass Bonferroni correction for the number of comparisons. The outstanding pattern indicated associations between a different pair of networks (network 10, anterior limbic; network 16 - DMN core) within DLPFC as related to the level of subjective detail in thoughts. Coupling between signals from these networks was associated with levels of detail in the 1-back task $(F(1,135)=14.014, p=.0003)$. The same equivalence analysis for this effect showed that the relationship between this interaction and detail in the 0-back was potentially of a comparable size and so could not be dismissed as a null finding. Additionally, the effect of this interaction on off-task thought in the DLPFC in both tasks was also too large to dismiss as definitely null. This means that the relationship between detailed thought in the 0-back, and task-related thought in both tasks, and the interaction between network 10 and network 16 within DLPFC was not statistically significant but was not significantly equivalent to 0, suggesting these relationships are too uncertain to draw firm conclusions. Post-hoc analysis showed that the correlation between these network components in DLPFC was positively related to detailed thought in the 0-back and negatively related to it in the 1-back (see Supplementary Figure 7). Similarly, this same interaction was related negatively to off-task thought in the 0-back and positively in the 1-back. This suggests that while this region was not identified as related to detail during task performance, there may be signals in this region that also describe the task relevant moderation of levels of detail, and it cannot be ruled out that these same signals relate to off-task thought.

Next, we repeated this analyses using bilateral parietal regions linked to on-task thought in Experiment 1 as the regions-of-interest (see Methods for explanation,

Figure 2 for the regions-of-interest, and Supplementary Table 3 for equivalence results). This found no comparable evidence that integration of distributed neural signals in these regions of parietal cortex are linked to patterns of experience. Finally, we repeated the whole brain analysis from Experiment 1 looking at the neural correlates of the other components of experience identified by PCA. This revealed one significant effect: reports of detailed thought was positively associated with neural signals in the posterior cingulate cortex in the harder 1-back task than in the easier 0-back task (see Supplementary Figure 6). Taken together these supplementary analyses show that (i) off-task thought was the only pattern of experience that was associated with clear task differences in its association with neural activity in the left DLPFC during task performance (Experiment 1) and (ii) the association between signals from the posterior DAN and the lateral DMN within DLPFC only are specifically related to the prioritisation of personally relevant information when external demands are reduced (Experiment 2).
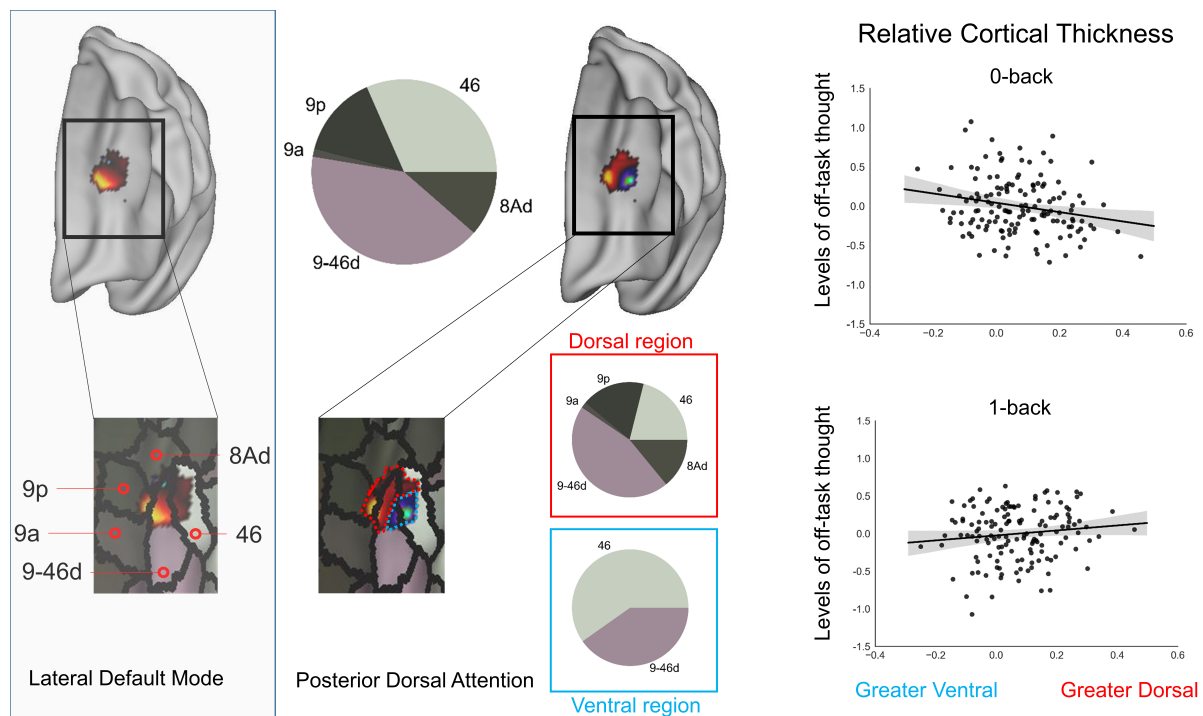
Figure 4. The structure of left DLPFC supports individual differences in prioritising off-task thought. Characterisation of the region of left DLPFC using a multimodal parcellation scheme (Glasser et al., 2016) demonstrates it encompasses region BA 9/46d, 9, 46, and 8Ad. The amount of overlap with each parcel of the Glasser atlas (Glasser et al., 2016) is shown by the pie charts, both for the region as a whole and for each sub-region (dorsal: red box, ventral: blue box). Relatively greater cortical thickness in a region negatively related to Yeo 5 (posterior dorsal attention network) was linked to more off-task thought when task demands are lower. This relationship is shown in the scatterplots.

4.4 Discussion

Our study combined multiple neuroimaging methods to demonstrate a role for left DLPFC in the prioritisation of personally relevant information in situations of low demands. To capture situations when individuals prioritise personally relevant thoughts when environmental demands are lower, we used a paradigm in which the low demand condition was associated with greater off-task thought (Konishi et al., 2015; Medea et al., 2016; Sormaz et al., 2018). Experiment 1 found that within this context neural signals in left DLPFC were associated with off-task thought when task demands are lower, and on-task thought when demands are higher. Importantly, this pattern contrasted with neural signals within a parietal aspect of the DAN, which showed a positive association with on-task thought in both tasks. Examining neural processing within the left DLPFC, Experiment 2 found that the capacity of an individual to generate off-task thought in the low demand condition was related to the degree of decoupling of neural signals arising from regions of posterior DAN, and involved in external task focus, from those from the lateral DMN. Further underlining the role of the DLPFC in off-task thought when environmental demands are reduced, we found that increases in cortical thickness in regions negatively related to task-relevant signals, relative to those positively linked to the posterior DAN, were linked to greater off-task thought. Together this pattern indicates that (a) under circumstances when off-task thought is high, periods of greater neural activity within the left DLPFC are linked to the emergence of increased personally relevant off-task thought and (b) that individuals who exhibit this capacity most clearly show a greater separation of functional signals between those linked to external task focus (the posterior DAN) and lateral regions of the DMN. Together these provide converging support for the involvement of DLPFC in the process of prioritising cognition that matches the demands of a particular context.

One important implication of these findings is that they provide resolution to a long-standing debate within the literature on mind-wandering. It is currently unclear whether executive control suppresses (McVay & Kane, 2010), or facilitates off-task thinking (Smallwood, 2010), with behavioural evidence consistent with both perspectives (Levinson et al., 2012; McVay & Kane, 2009; Rummel & Boywitt, 2014; Unsworth & McMillan, 2013). Critically, behavioural studies alone may struggle to dissociate these positions because periods of off-task thinking during behavioural

tasks measuring executive control are linked to poor performance (Mrazek et al., 2012; Unsworth & Robison, 2016). Our neural evidence suggests that these are complementary (Christoff et al., 2016), rather than contradictory accounts, since we found that focusing on a task, or imagining different people, times, and places, depends on shared neural processes in left DLPFC. Our individual difference analysis suggests DLPFC helps prioritise off-task thought via reductions in the processing of external task-relevant signals (Smallwood, Beach, et al., 2008), a position supported by evidence that lesions to this region prevent patients ignoring external sensory input (Kam et al., 2018). In mechanistic terms, therefore, our data suggests DLPFC may contribute to the decoupling of attention from external input that is thought to be necessary for efficient processing of self-generated information (Smallwood, 2013b).

Studies from humans and non-human primates suggest DLPFC prioritises task-relevant information in a context-dependent manner (Badre & Nee, 2017; de la Vega et al., 2017; Dosenbach et al., 2008; Petrides, 2005) - monitoring signals from internal and external sources, emphasising those with greatest relevance to current goals (Jiang, Wagner, & Egner, 2018; Petrides, 2005). Our study suggests humans have co-opted this process, allowing us to explicitly prioritise processes such as daydreaming, rather than less compelling events in the here-and-now. Although the ability to imagine different times and places is important (Baird et al., 2012), failure to appropriately suppress self-generated experiences causes problems in education (Smallwood, Fishman, et al., 2007), the workplace (McVay & Kane, 2009), and while driving (He et al., 2011). Accordingly, managing when we let our minds wander requires cognition to be regulated in a context-dependent manner, and our study highlights left DLPFC is important in this process.

Before closing it is worth noting that as well as highlighting the left DLPFC in the process through which off-task thought is prioritised in a context appropriate manner, our data also implicate the DMN in how vivid and detailed experience is. Prior studies looking at population level variation in self-reports of the level of detail in patterns of ongoing thought show they are linked to neural processes within the DMN (Gorgolewski et al., 2014; Smallwood et al., 2016). In this context, the current study provides both online evidence (see Supplementary Figure 6) and individual difference analysis that complements our prior studies (see Supplementary Figure 7). More generally, the view of the DMN as important for the level of detail in experience is

consistent with prior studies that suggest details in memories are represented in posterior elements of the large scale network, including both the posterior cingulate (Richter et al., 2016) and angular gyrus (Bonnici, Richter, Yazar, & Simons, 2016; Davey et al., 2015). Moreover, structural abnormalities in the posterior cingulate that emerge in dementia contribute to deficits in detail (Irish et al., 2014) and problems in generating a vivid scene in imagination (Irish et al., 2015). Intriguingly, functional connections between the hippocampus and posterior cingulate cortex, which are associated with more detailed experiences in healthy individuals (Smallwood et al., 2016), is dysfunctional in dementia populations (O'Callaghan, Shine, Hodges, Andrews-Hanna, & Irish, 2019). These observations provide converging evidence for a role of the DMN in features of how an experience is represented, such as its subjective detail. Together this emerging literature provides the basis for a hypothesis of the contribution of the DMN in patterns of ongoing thought that future studies could explore. In particular, it will be helpful to use measures of neural function and experience across a wide range of situations to identify how broadly this relationship holds and identifying the causal role of DMN regions by studying populations with deficits within this system (such as Alzheimer's Disease) and by creating virtual lesions within this system in normal populations using techniques like transcranial stimulation (Kam et al., 2018).

Although our study provides important evidence implicating left DLPFC in the process through which we appropriately prioritise the nature of ongoing thought in a context dependent manner, there are a number of important issues that remain unresolved. First, it is unclear whether the context dependent nature of the role of left DLPFC in ongoing thought, conveys a behavioural advantage. Our study is unable to address this issue, in part, because although we found a consistent change in off-task thought across the 0-back and 1-back conditions in both experiments, we only observed a modulated pattern of behaviour in the larger behavioural study. It is possible that this absence of a difference occurs because of the differences of the testing environment across the two experiments. Regardless of the reason for the absence of a behavioural difference in the scanner, in the future it will be important to determine whether left DLPFC is also important in facilitating behavioural efficiency across a range of different task contexts. Second, our study highlights left DLFPC as important in modulating ongoing thought across situations that on average vary in the

degree to which they depend on continual focus on task relevant information (Experiment 1) and that the degree to which individuals achieve this is related to neural patterns in the left DLPFC at rest (Experiment 2). In the future it will be important to use techniques that causally influence neural signals within this region (such as transcranial magnetic stimulation), or populations with lesions in this cortical region, to explicitly address whether this region plays a causal role in how we exert control on our thoughts in order to ensure they are as aligned as possible with our goals.

4.5 Methods

4.5.1 Subject Details

See Table 1 for a full description of the sample in both experiments. In Experiment 1, 63 participants took part in the online task-based fMRI study. After excluding participants (see Method Details) 60 participants (37 females, mean age=20.17 years, S.D=2.22 years) remained for data analysis. 34 participants from this sample were scanned for the data used in Sormaz et al. (2018) (Sormaz et al., 2018). A group of 157 young adults were recruited for the resting state fMRI and laboratory part of this study. After excluding participants (see Method Details) 146 participants remained for data analysis (89 females, mean age=20.21 years, S.D=2.49 years). These data have been used before by Turnbull et al. (2019)(Adam Turnbull et al., 2019). Of these participants, 39 also participated in Experiment 1. All participants were native English speakers, with normal/corrected vision, and no history of psychiatric or neurological illness. All participants were acquired from the undergraduate and postgraduate student body at the University of York. Both experiments were approved by the local ethics committee at both the York Neuroimaging Centre and the University of York's Psychology Department. All volunteers gave informed written consent and were compensated in either cash or course credit for their participation. A summary of the demographics can be seen in Table 1.

Experiment	Task-based fMRI	Resting state fMRI	Cortical thickness MRI
Number of participants	60	146	142
Age (years)	M=20.17, S.D.=2.22	M=20.21, S.D.=2.49	M=2.23, S.D.=2.47
Gender	37 F, 23 M	89 F, 57 M	86 F, 56 M

Table 1. Participant demographics for each experiment. 39 participants performed both the resting state and task-based portions of this study. Cortical thickness analysis was performed in the same group as the resting-state analysis, but four participants were excluded as their structural data did not pass quality control.

4.5.2 Multi-Dimensional Experiential Sampling (MDES)

Experience was sampled in a task paradigm that alternated between blocks of 0-back and 1-back in order to manipulate attentional demands and working memory load (Figure 1). Non-target trials in both conditions were identical, consisting of black shapes (circles, squares, or triangles) separated by a line. In these trials the participant was not required to make a behavioural response. The shapes on either side of the line were always different. The colour of the centre line indicated to the participant the condition (0-back: blue, 1-back: red; mean presentation duration=1050ms, 200ms jitter). The condition at the beginning of each session was counterbalanced across participants. Non-target trials were presented in runs of 2-8 trials (mean = 5) following which a target trial or multidimensional experience sampling (MDES) probe was presented.

During target trials, participants were required to make a behavioural response on the location of a specific shape. In the 0-back condition, on target trials, a pair of shapes were presented (as in the non-target trials), but the shapes were blue. Additionally, there was a small blue shape in the centre of the line down the middle of the screen. Participants were required to press a button to indicate which of the large shapes matched the central shape. This allowed participants to make perceptually-guided decisions so that the non-targets in this condition do not require continuous monitoring. In the 1-back condition, the target trial consisted of two red question marks either side of the central line (in place of the shapes). There was a small shape in the centre of the screen as in the 0-back condition, but it was red. Participants had to indicate via button press which of the two shapes from the previous trial the central

shape matched. Therefore, the decisions in this condition were guided by memory and so in this condition non-target trials had to be encoded to guide this decision.

The contents of ongoing thought during this paradigm were measured using Multi Dimensional Experience Sampling (MDES). MDES probes occurred instead of a target trial on a quasi-random basis. When a probe occurred the participants were asked how much their thoughts were focused on the task, followed by 12 randomly shuffled questions about their thoughts (see Supplementary Table 1). All questions were rated on a scale of 1 to 4.

In the online task-based fMRI part of this study (Experiment 1), participants completed this task while undergoing fMRI scanning. Each run was 9-minutes in length and there were four runs per scanning session. In each run, there was an average of six thought probes (three in each condition), so that there were on average 24 (SD=3.30, mean=12 in each condition) MDES probes in each session. Two participants had one run dropped due to technical issues, leaving them with 18 MDES probes each.

In the behavioural laboratory (Experiment 2), to derive a reasonable stable estimate of each individual's patterns of thought, participants performed the task on three separate days in sessions that lasted around 25 minutes. In each session, the were eight blocks. In total, an average of 30.7 MDES probes occurred (SD=5.7, mean=15.4 in each condition). In the laboratory, accuracy was significantly greater (t(145)=9.487, p<.001) and reaction time significantly faster (t(145)=14.362, p<.001) in the easier 0-back task. This effect was not found in either measure during fMRI scanning (accuracy: t(59)=0.369, p=.714, rt: t(59)=0.052, p=.958, see Supplementary Figure 1).

4.5.3 Resting-state (Experiment 2)

In the scanner, participants completed a 9-minute eyes-open resting state scan during which there was a fixation cross on-screen. Participants were instructed to look at the fixation cross and try to stay awake.

4.5.4 fMRI Acquisition

All MRI scanning was carried out at the York Neuroimaging Centre. The scanning parameters were identical for both the resting state and online task-based

scans. Structural and functional data were acquired using a 3T GE HDx Excite MRI scanner with an eight-channel phased array head coil tuned to 127.4 MHz. Structural MRI acquisition was based on a T1-weighted 3D fast spoiled gradient echo sequence (TR=7.8s, TE=minimum full, flip angle=20º, matrix size=256x256, 176 slices, voxel size =1.13x1.13x1mm). Functional data were recorded using single-shot 2D gradient echo planar imaging (TR=3s, TE=minimum full, flip angle=90º, matrix size=64x64, 60 slices, voxel size=3mm isotropic, 180 volumes). A FLAIR scan with the same orientation as the functional scans was collected to improve coregistration between scans.

4.5.5 Data Pre-processing: Online Task-based fMRI (Experiment 1)

Two participants were excluded for falling asleep. Task-based 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). The functional data were pre-processed and analysed using the FMRI Expert Analysis Tool (FEAT). The individual subject analysis first involved motion correction using MCFLIRT and slice-timing correction using Fourier space time-series phase-shifting. After coregistration to the structural images, individual functional images were linearly registered to the MNI-152 template using FMRIB's Linear Image Registration Tool (FLIRT). Functional images were spatial smoothed using a Gaussian kernel of FWHM 6mm, underwent grand-mean intensity normalisation of the entire 4D dataset by a single multiplicative factor, and both highpass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma=100s); and Gaussian lowpass temporal filtering, with sigma=2.8s. An additional participant was excluded for having relative motion >0.2mm in more than 50% of runs (three participants total excluded).

4.5.6 Data Pre-processing: Resting-state fMRI (Experiment 2)

Preprocessing of the resting state fMRI data was carried out using the SPM software package (SPM Version 12.0, http://www.fil.ion.ucl.ac.uk/spm/) based on the MATLAB platform (Version 16.a, https://uk.mathworks.com/products/matlab.html). The individual subject analysis first involved motion correction with six degrees of freedom and slice-timing correction. Structural images were coregistered to the mean functional image via rigid-body transformation, segmented into grey/white matter and

cerebrospinal fluid probability maps, and images were spatially normalized to the MNI-152 template. Functional images were spatially smoothed using an 8mm Gaussian kernel; a slightly larger kernel was chosen to account for the increased sensitivity of functional connectivity analyses to signal-to-noise (SNR) issues. Due to the additional problems associated with motion in functional connectivity analyses (Power et al., 2012); additional denoising procedures were carried out using the CONN functional connectivity toolbox (Version 17.f, https://www.nitrc.org/projects/conn, (Whitfield-Gabrieli & Nieto-Castanon, 2012)). An extensive motion correction procedure was carried out, comparable to that previously reported in the literature (Ciric et al., 2017). In additional to the removal of six realignment parameters and their second-order derivatives using a GLM (Friston, Williams, Howard, Frackowiak, & Turner, 1996), a linear detrending term was applied as well as the CompCor method with five principle components to remove signal from white matter and cerebrospinal fluid (Behzadi et al., 2007). Volumes affected by motion were identified and scrubbed if motion exceeded 0.5mm or global signal changes were larger than z=3. Eleven participants that had more than 15% of their data affected by motion were excluded from the analysis (Power et al., 2014). Global signal regression was not used in this analysis due to its tendency to induce spurious anti-correlations (K. Murphy, Birn, Handwerker, Jones, & Bandettini, 2009; Saad et al., 2012). A band-pass filter was used with thresholds of 0.009 and 0.08Hz to focus on low frequency fluctuations (M. D. Fox et al., 2005).

4.5.7 Principal Component Analysis

Behavioural analyses were carried out in SPSS (Version 24.0, 2016). The scores from the 13 experience sampling questions were entered into a principal component analysis (PCA) to describe the underlying structure of the participants' responses. Following prior studies (Konishi et al., 2017; Ruby, Smallwood, Engen, et al., 2013; Smallwood et al., 2016) we concatenated the responses of each participant in each task into a single matrix and employed a PCA with varimax rotation. Four components were selected based on the inflection point in the scree plot (see Supplementary Figure 3). These were defined as Task-relatedness, Detail, Modality, and Emotion of thought based on their question loadings. These loadings for both the scanner and laboratory components can be seen in Supplementary Figure 2. Several analyses were performed to assess the similarity between PCA analyses in the laboratory and

in the scanner. The PCA loadings for the off-task components were correlated across experimental conditions (Off-task: r(11)=.882, p<.001: Supplementary Figure 2). The off-task PCA scores in each task condition were also correlated within the equivalent task condition for the 39 participants who took part in both parts of the experiment (Off-task: 0-back r(37)=.475, p=.002, 1-back r(37)=.389, p=.014). Finally, paired t-tests were carried out to assess the differences in the off-task component between the 0-back and 1-back conditions (see results).

4.5.8 Task-based fMRI Analysis (Experiment 1)

Task-based analyses were carried out in FSL (FSL version 4.1, http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FEAT/). A model was set up for off-task thought by including four explanatory variables (EVs) as follows: EVs 1 and 2 modelled time periods in which participants completed the 0-back and 1-back task conditions; EVs 3 and 4 modelled the three thought probes in each condition, respectively, with a time period of 6 seconds prior to the MDES probe and the scores for the task-related component. This was convolved with the hemodynamic response function. We chose to use 6 seconds as it was the longest temporal interval within which no behavioural response occurred. Contrasts were included to assess brain activity that related to each task, as well as each component of thought. For the tasks, 0-back>1-back and 1-back>0-back contrasts were included. For the thoughts, main effects (positively or negatively related to thoughts in both conditions) and comparisons (activity related to thoughts in 0-back>thoughts in 1-back and vice versa) were included. The four runs were included in a fixed level analysis to average across the activity within an individual. Group level analyses were carried out using a cluster-forming threshold of Z>3.1 and a whole-brain correction at p<.05 FWE-corrected. In these analyses we followed best practice as described by Eklund and colleagues (Eklund et al., 2016). Specifically, we used FLAME, as implemented in FSL, applied a cluster forming threshold of Z = 3.1, and corrected these at p <.05 (corrected for family wise error rate using random field theory). Average motion was included at the group level to additionally control for effects relating to this nuisance variable. This model was repeated for each component as a follow-up analysis (see below). Brain figures were made using BrainNet Viewer (Xia et al., 2013), plots made using matplotlib in Python (version 3.6.5). Meta-analytic decoding used Neurosynth (Yarkoni et al., 2011) to find terms most commonly associated with our neural maps in the literature. This platform

collects and synthesises results from many different research studies, and identifies the terms associated most often with each region of the brain.

4.5.9 Resting-state Analysis (Experiment 2)

To understand whether the interaction of signals from the whole brain were implicated in the control of off-task thought within this region, we performed a modified version of an echoes analysis. In the original analysis (Leech et al., 2012), an independent component analysis was performed within a masked region of the brain, to identify different components within the region from its timeseries. These components represented voxels that grouped together in terms of their temporal signals, and they were shown to represent different functional networks within a single region of the brain. In our analysis, instead of identifying these components in a data-driven way, we used 17 well-established networks from the literature. The timecourse from these networks were correlated with the timecourse within the left DLPFC to identify components within this region that represented each network. To do this, the 17 Yeo network masks (Thomas Yeo et al., 2011) were binarised and merged into a single 4D nifti file. In order to reduce statistical bias from the region itself, the corresponding region (left DLPFC) was masked out of this nifti. These networks were entered into a dual regression that extracted the timeseries from within each Yeo network and subsequently regressed these against each subjects 4D dataset within the left DLPFC. Thus, for each network, each voxel in the left DLPFC was given a value for how much it represented the Yeo network in question, to make up 17 different components within this region that each represented one of the Yeo networks. These maps were again merged into a single file and entered into the first step of a second dual regression in order to extract the timeseries of each Yeo 17 echo or component. FSL Nets (v0.6) was used to extract these timeseries and produce a matrix of interactions defined by the partial correlation between each set of echoes. These interactions were entered into a model as dependent variables to model their relationship to the average component scores (e.g. task-relatedness) in each task from the laboratory. We inspected each component, and if no voxels were significantly related to the Yeo network in question it was deemed to likely represent noise and its interactions were excluded from the analysis. An alpha value of $p < .05/17$ was used to account for family-wise error in these analyses. The average scores from each task were included as independent variables in the model (MANOVA), as well as the

interaction between the scores in each task, and age, gender, and mean motion in order to additionally control for the effect of these covariates of no interest. This was used to identify any specific network interactions that could be predicted by the thoughts in either task.

Several analyses were performed to assess the specificity of this result. First, we repeated this masked network interaction analysis with the other components of thought (Detail, Modality, and Emotion: see Supplementary Figure 2), and found only one significant effect within the model for Detailed thought that passed Bonferroni correction, with the interaction between Yeo networks 10 and 16 within the DLPFC region-of-interest significantly related to the level of Detail in participants' thoughts in the 1-back task ($F(1,135)=12.792$, $p=.000484$). Next, we repeated the analysis from Experiment 1 using the other components in turn (i.e. the PCA scores from Detail, Modality, and Emotion rather than Off-task). This revealed a region of posterior cingulate cortex whose neural signature was consistent with a task-dependent association with the level of detail in ongoing experience, in a similar way to the DLPFC was related to off-task thought (see Supplementary Figure 6). To see whether it regulated detail using a similar mechanism, we repeated the masked connectivity analysis described above on this region and there was no individual interaction that passed Bonferroni correction. No other components of experience showed a brain region with a pattern consistent with context regulation, but there were several results related to levels of thought in a non-task-dependent manner (see Supplementary Figure 9). Third, we repeated the connectivity analyses from Experiment 2 using the whole brain, rather than limiting the analysis to the DLPFC. This analysis found no significant relationships between network interactions and off-task thought in any conditions, suggesting the association between the interaction of the dorsal attention network and the default mode network with off-task thought is not a property of the broader cortical mantle. Fourth, we explored whether this same analysis would identify similar effects in regions important for on-task thought regardless of the task (lateral parietal regions: see Figure 2). This analysis revealed no significant relationships that passed Bonferroni correction suggesting that the relationships between network interactions in DLPFC and off-task thought identified in our prior analyses were unique to regions that responded in a manner that was task-dependent.

Finally, to test whether the specific relationships we found (between the network 5-network 17 interaction and off-task thought, and the network 10-network 16 interaction and detailed thought) were truly unique to these conditions, we performed a series of equivalence analyses. These were done using the TOST equivalence test for correlations described in Lakens (2017) (Lakens, 2017). We extracted the strength of the relationship in our significant result (between the interaction of network 5 and 17 and off-task thoughts in the 0-back, and between the interaction of network 10 and 16 and detailed thought in the 1-back) and used these as the upper and lower bounds to see if there were any effects of this size under the other conditions. All of these tests using the network 5-network 17 interaction were significant, suggesting the correlations between this interaction and the thoughts under other conditions were equivalent to 0 and represent true null findings (see Supplementary Table 3). This suggests that this interaction is specifically able to predict off-task thoughts in the 0-back task within DLPFC. The network 10-network 16 interaction was able to significantly predict detail within the DLPFC in the 1-back task. An equivalence analysis suggested that the effect in the 0-back was of equivalent size and cannot be dismissed as a null effect. Interestingly, this also involves the default mode network, and a post hoc analysis showed that the relationship to detail was task-dependent (see Supplementary Figure 7). The relationship between this interaction and off-task thought also was not significant using this equivalence test, so this relationship cannot be dismissed as null. Post-hoc analyses showed that this relationship was also task-dependent (see Supplementary Figure 7).

All data were mean centred before analysis. Chord diagrams were made using R: these represent the strength of the relationship between each interaction and the thoughts. Parameter estimates were extracted from the MANOVA so that each interaction had a beta-weight representing how strongly it related to the thoughts as part of the model. These were used to create chord diagrams that show the strength of these relationships (in the size of the chords) and their direction (blue is negative, red is positive).

4.5.10 Cortical Thickness Analysis

After identifying that the DAN echo appeared to span multiple regions, we performed a follow up structural analysis that looked at whether the difference in

cortical thickness between DAN-negative and DAN-positive regions also related to the levels of off-task thoughts. FreeSurfer was used to estimate vertex-wise cortical thickness (5.3.0; https://surfer.nmr.mgh.harvard.edu), using an automated surface reconstruction scheme described in detail elsewhere (Dale, Fischl, & Sereno, 1999; Fischl & Dale, 2000; Fischl, Liu, & Dale, 2001; Fischl, Sereno, & Dale, 1999). The following processing steps were applied: intensity normalisation, removal of non-brain tissue, tissue classification and surface extraction. Cortical surfaces were visually inspected and corrected if necessary. Cortical thickness was calculated as the closest distance between the grey/white matter boundary and pial surface at each vertex across the entire cortex. A surface-based smoothing with a full-width at half maximum (FWHM) = 20 mm was applied. Surface alignment based on curvature to an average spherical representation, fsaverage5, was used to improve correspondence of measurement locations among subjects. 142 of the 146 participants used in the previous analysis had cortical thickness extracted in a way that passed visual quality control. The scores for the DAN-negative region were subtracted from the DAN-positive region to give a difference score. This was entered into a MANOVA, with the off-task scores in each task as the dependent variables, as well as age and gender as covariates of no interest. All data were mean centred before analysis. Overlaps were calculated and displayed with Brodmann and Glasser (Glasser et al., 2016) labels using Connectome Workbench, with labels being acquired from the BALSA database (Van Essen et al., 2017).

Chapter 5 – Word up – experiential and neurocognitive evidence for associations between autistic symptomology and a preference for thinking in the form of words

This chapter is adapted from: Turnbull, A., Garfinkel, N., Ho, N., Critchley, H. D., Bernhardt, B., Jefferies, E., & Smallwood, J. (2020). Word up – experiential and neurocognitive evidence for associations between autistic symptomology and a preference for thinking in the form of words. *Cortex* (in press).

5.1 Abstract

Autism symptomology has a profound impact on cognitive and affective functioning, yet we know relatively little about how it shapes patterns of ongoing thought. In an exploratory study in a large population of neurotypical individuals, we used experience sampling to characterise the relationship between ongoing cognition and self-reported autistic traits. We found that with increasing autistic symptom score, cognition was characterised by thinking more in words than images. Analysis of structural neuroimaging data found that autistic traits linked to social interaction were associated with greater cortical thickness in a region of lingual gyrus (LG) within the occipital cortex. Analysis of resting state functional neuroimaging data found autistic traits were associated with stronger connectivity between the LG and a region of motor cortex. Importantly, the strength of connectivity between the LG and motor cortex moderated the link between autistic symptoms and thinking in words: individuals showing higher connectivity showed a stronger association between autistic traits and thinking in words. Together we provide behavioural and neural evidence linking autistic traits to the tendency to think in words which may be rooted in underlying cortical organisation. These observations lay the groundwork for research into the form and content of self-generated thoughts in individuals with the established diagnosis of autism.

5.2 Introduction

Autism Spectrum Disorder (ASD) encompasses a set of neurodevelopmental conditions that share core psychological, sensory, and social characteristics and that begin within the first few years of life (Ozonoff, Heung, Byrd, Hansen, & Hertz-Picciotto, 2008). Autism is expressed in a wide range of symptoms including differences in sensory processing (Leekam, Nieto, Libby, Wing, & Gould, 2007), executive function (Craig et al., 2016), attention (Moriuchi, Klin, & Jones, 2016), imagination (Crespi, Leach, Dinsdale, Mokkonen, & Hurd, 2016), and social functioning (Baron-Cohen, 2000; Garfinkel et al., 2016; Tager-Flusberg, Paul, & Lord, 2005). In the sensory domain, autistic individuals often find sensory information overwhelming and unusually aversive (Baron-Cohen, Ashwin, Ashwin, Tavassoli, & Chakrabarti, 2009), and in the motor domain, autistic individuals show alterations in movement, such as gait (Kindregan, Gallagher, & Gormley, 2015) and an increased tendency for repetitive motoric action (Militerni, Bravaccio, Falco, Fico, & Palermo, 2002), potentially as a countermeasure to the hypersensitivity to sensory stimuli. In terms of higher order processes, autistic individuals show evidence of impaired or delayed development of an intuitive "theory of mind" (Baron-Cohen, Leslie, & Frith, 1985). Although we have a relatively clear understanding of how autistic traits relate to performance on structured neurological tasks (Kenworthy, Yerys, Anthony, & Wallace, 2008), we know substantially less about how these traits influence patterns of ongoing thought. In this exploratory study, we used experience sampling to explore how autistic traits within a neurotypical population relate to the types of thoughts participants experienced within a laboratory setting.

Studying autistic traits in neurotypical individuals is a popular technique that enables researchers to leverage larger, easier to access populations and gain insights into the differences that may be seen in autism (Barttfeld et al., 2013; Di Martino, Shehzad, et al., 2009; Jakab et al., 2013; Koolschijn, Geurts, Van Der Leij, & Scholte, 2015; Wallace et al., 2012). It is possible that if autism is an example of "neurodiversity", then autistic traits historically considered as part of a "disorder" are actually examples of normal variation in neurocognitive functioning (T. Armstrong, 2015; Baron-Cohen, 2017). Individuals diagnosed with ASD could therefore show differences in specific domains that are sufficiently far from those seen in the population "on average" as to be considered clinically meaningful. This framework has

received support in ethical domains, as it encourages a less stigmatising approach to improving the quality of life in autistic individuals without the harmful idea that they need to be "cured" (S. M. Robertson, 2009). It also highlights the areas in which autistic individuals show positive variation, such as attention to detail and pattern-detection (Baron-Cohen, 2006). This approach is also supported by genetic evidence that suggests autistic traits in neurotypical individuals share a common aetiology with those seen in clinical populations (Lundström et al., 2012). Together this evidence suggests studying these autistic traits in neurotypical samples like the one used here can provide information about the mechanisms behind these traits that are shared by autistic individuals.

Experience sampling allows the investigator to capture the patterns of thought that occupy individuals in the laboratory and in daily life (Smallwood & Schooler, 2015). This technique has established that spontaneous thought is a heterogeneous state that contains replicable components that can be reliably identified across individuals (Martinon, Smallwood, et al., 2019; Poerio et al., 2017; Smallwood & Schooler, 2015; Sormaz et al., 2018; H.-T. Wang, D. Bzdok, et al., 2018). In the current study we used Multi-Dimensional Experience Sampling (MDES) which directly examines this heterogeneity by asking individuals to report on multiple features of their experience. Across multiple studies we have found that decompositions of MDES data reveals latent components that describe how on-task experience is, whether it is vividly detailed, its modality (i.e. whether it is in the form of images or words), and its emotional tone (Sormaz et al., 2018; Adam Turnbull et al., 2019). Studies show that these components correlate with measures of intelligence, well-being, and clinical symptomatology (M. S. Franklin et al., 2017; Adam Turnbull et al., 2019; Vatansever et al., 2018; H.-T. Wang, G. Poerio, et al., 2018). In addition, MDES highlights the important role of task context on the nature of ongoing experience. For example, tasks with lower levels of cognitive demand produce fewer on-task thoughts (Konishi et al., 2017; Smallwood, Ruby, et al., 2013) and increase individuals' tendencies to think deliberately about other things (Seli, Konishi, Risko, & Smilek, 2018; Seli et al., 2016b). In our study, we explored the association between autism and the patterns of thought highlighted by MDES using a paradigm that moderates task demands by inducing a working memory load.

Preliminary evidence suggests that autistic traits could have an important influence on patterns of ongoing thought. Studies demonstrate that individuals with ASD have deficits in imagination (Crespi et al., 2016) and future thinking (Crane, Lind, & Bowler, 2013; Lind & Bowler, 2010), and across different cultures, prospection makes up a large proportion of daily experience (Baird et al., 2011; Iijima & Tanno, 2012; Ruby, Smallwood, Engen, et al., 2013; Song & Wang, 2012; Stawarczyk et al., 2013; Stawarczyk, Majerus, Maj, et al., 2011). Autistic individuals exhibit deficits in executive function (Craig et al., 2016) and attention switching (Reed & McCarthy, 2012; Stoet & Lopez, 2011), and differences in these aspects of cognitive control have been linked to changes in the flexibility with which self-generated thoughts occur (McVay & Kane, 2010, 2012a, 2012b; McVay et al., 2009; Robison & Unsworth, 2015; Rummel & Boywitt, 2014; Adam Turnbull et al., 2019; Unsworth & McMillan, 2013). More specifically, there is a range of literature suggesting that differences in autism can be attributed to an inability to adapt behaviour and thinking flexibly to the current context using clues from the external environment (Vermeulen, 2015). Studies using the task design from the current study have shown that typically developing individuals adapt their patterns of thoughts based on the demands of the task (A Turnbull et al., 2019), a process that may show a negative relationship to autistic traits.

Finally, it has been hypothesised that a key component of ASD is that individuals with this condition think in pictures (Kana, Keller, Cherkassky, Minshew, & Just, 2006; Kunda & Goel, 2011). This theory is motivated by the fact that autistic individuals show relatively intact or enhanced abilities on a range of visuospatial tasks, including the Block Design subset of the Weschler Intelligence Scales (D. J. Siegel, Minshew, & Goldstein, 1996), the embedded figures task (Damarla et al., 2010; Jolliffe & Baron-Cohen, 1997), and Raven's Progressive Matrices (RPM) (Dawson, Soulières, Ann Gernsbacher, & Mottron, 2007). A study using a similar typically developing undergraduate population to in the current study found that autistic traits in two subscales of the autism quotient (AQ) were related to improved RPM performance, and this prediction was stronger for visuospatial rather than verbal-analytic items (Fugard, Stewart, & Stenning, 2011). Another study suggests enhanced visuospatial processing in a range of tasks can be identified related to the AQ in neurotypical individuals (Grinter, Van Beek, Maybery, & Badcock, 2009). Autistic individuals also complete semantic tasks with a greater accuracy when matching pictures to words

rather than words to words (Kamio & Toichi, 2000). These results are often interpreted as an overall preference for pictures over words in autistic cognition (Kana et al., 2006), especially when considered alongside deficits in language processing (Eigsti, de Marchena, Schuh, & Kelley, 2011) and anecdotal evidence for thinking in pictures (Grandin, 2006). A review of tasks that are typically done verbally that can be done visually suggests mixed evidence for a preference for these strategies (Kunda & Goel, 2011). For example, autistic individuals showed no articulatory suppression during a dual-task experiment, suggesting less reliance on inner speech (Whitehouse, Maybery, & Durkin, 2006), but use verbal strategies when maintaining information in working memory but not during planning (D. M. Williams, Bowler, & Jarrold, 2012). Taken together these results have been interpreted as relating to an improved ability to see patterns due to "weak central coherence" (Shah & Frith, 1993), a tendency in typically developing individuals to look for additional meaning when there is none (Jolliffe & Baron-Cohen, 1997), or a general preference for thinking in pictures (Kana et al., 2006). The present study will therefore look for relationships between overall levels of different dimensions of ongoing thought as well as their context-specific regulation to assess whether there are identifiable links to autistic traits in a neurotypical sample of undergraduates.

Importantly, several recent studies demonstrate the feasibility of experience sampling in people diagnosed with ASD (Chen, Bundy, Cordier, & Einfeld, 2014; Chen, Cordier, & Brown, 2015; Cordier, Brown, Chen, Wilkes-Gillan, & Falkmer, 2016), showing that autistic individuals respond at a comparable rate and demonstrating that it is a reliable method for identifying differences in thought patterns during daily life. The extension of MDES to examine autistic traits in a normative population, therefore, provides important information about how ongoing thought relates to autistic traits that could act as a foundation for extending the method into a more clinically relevant population.

Since measures like MDES are subjective, studies of ongoing thought often combine these with objective metrics from behaviour or neuroimaging (Martinon, Smallwood, et al., 2019). This process of triangulation offers the opportunity to confirm the subjective reports using a more objective metric, and in the current study enables the MDES data to be understood in the context of contemporary accounts of neurocognitive alterations in autism. Prior studies of autism highlight structural and

functional differences in visual (Gaffrey et al., 2007; Hyde, Samson, Evans, & Mottron, 2010; Villalobos, Mizuno, Dahl, Kemmotsu, & Müller, 2005), auditory (Bomba & Pang, 2004; Bruneau, Roux, Adrien, & Barthélémy, 1999; Gervais et al., 2004), and motor cortices (Mostofsky, Burgess, & Gidley Larson, 2007; Nebel et al., 2014; Théoret et al., 2005), as well as regions of the brain implicated in social processes (Di Martino, Ross, et al., 2009; Gotts et al., 2012; Hadjikhani, Joseph, Snyder, & Tager-Flusberg, 2007; Kennedy & Courchesne, 2008a, 2008b; Lynch et al., 2013; Monk et al., 2009) (regions such as medial prefrontal cortex and lateral parietal cortices that are key nodes within the Default Mode Network; DMN). A meta-analysis of structural MRI studies found that there were both grey matter increases and decreases in autistic individuals. Increases were found in DMN regions such as the posterior cingulate and middle temporal gyrus, as well as visual regions including left lingual gyrus (LG) (Cauda et al., 2011). Regions with decreased grey matter included many regions adjacent to these, as well as the right amygdala and left precentral gyrus. Similarly, a meta-analysis of functional fMRI research found increases and decreases in activation in many of the same regions, largely dependent on the task being performed (Philip et al., 2012). In tasks requiring visual processing, for example, autistic individuals displayed greater activation in the thalamus, medial frontal gyrus, and caudate, but showed decreased activation in the cingulate, precentral gyrus, middle occipital gyrus, and left LG. Meta-analyses of functional connectivity have identified predominantly hyperconnectivity of cortical-cortical connections, and hypoconnectivity of subcortical-cortical edges (Di Martino et al., 2014). Studies extending these analyses to autistic traits in neurotypical populations are less common, and have had mixed findings, with some reporting similar structural and functional differences to those seen in autistic individuals (Di Martino, Shehzad, et al., 2009; Geurts, Ridderinkhof, & Scholte, 2013; von dem Hagen et al., 2010; Wallace et al., 2012), and some demonstrating null findings (Koolschijn et al., 2015).

In the current study, we reanalyse data from a cohort of healthy undergraduates for whom we have already described links between patterns of ongoing thought and a number of neural and behavioural metrics (Poerio et al., 2017; Adam Turnbull et al., 2019; Vatansever et al., 2018; Villena-Gonzalez et al., 2018). The current exploratory analysis examines the relationship between spontaneous thought and autistic traits in a neurotypical population. These individuals underwent both structural and resting

state MRI scanning, and performed a simple cognitive task in the laboratory on three different days in which MDES was used to measure patterns of ongoing thought. Our specific aim was to explore the relationship between autistic traits and (i) patterns of ongoing thought in the lab, and (ii) measures of structural and functional organisation of the cortex. Following this initial exploratory analysis, we conducted a post hoc examination of whether any underlying neural differences we observed explained the relationship we identified between autistic traits and patterns of ongoing thought in this neurotypical population.

5.3 Methods

5.3.1 Participants

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. The data presented here came from a cohort described in previous published work (Poerio et al., 2017; Adam Turnbull et al., 2019; Vatansever et al., 2018; Villena-Gonzalez et al., 2018; H.-T. Wang, D. Bzdok, et al., 2018). Ethical approval for this study was obtained from both the Department of Psychology, University of York, and the York Neuroimaging Centre ethics committees. All participants gave informed consent prior to taking part and were compensated with either payment or course credit for their participation. All participants were healthy, right-handed, native English speakers with no history of psychiatric or neurological illness, and these exclusion criteria were determined prior to data analysis. Out of this cohort, 199 participants (128 females, mean age=20.11, S.D.=2.24, range=18-31 years) completed the laboratory-based thought sampling experiment that was initially used to generate the thought components for this study. Of these, 181 participants (119 females, mean age=20.09, S.D.=2.22, range=18-31 years) completed the ASD symptomatology questionnaire and were included in the initial behavioural analysis. Finally, after exclusion for problems associated with MRI scanning (see below), 165 participants (110 female, mean age=20.16, S.D.=2.27, range=18-31) were entered into the cortical thickness analysis and 165 participants (108 female, mean age=20.07, S.D.=2.28, range=18-31) were entered into the resting state fMRI data analysis. No part of the study procedures was preregistered prior to the research being conducted.

5.3.2 Experimental Task and Experience Sampling

The experience sampling procedure was the same as reported in previous studies (Vatansever et al., 2018). Experience was sampled in a task paradigm that alternated between blocks of 0-back and 1-back in order to manipulate attentional demands and working memory load (see Supplementary Figure 1). The scripts for running this task can be found at: https://github.com/htwangtw/MindWanderingTask. Non-target trials in both conditions were identical, consisting of black shapes (circles, squares, or triangles) separated by a line. In these trials the participant was not required to make a behavioural response. The shapes on either side of the line were always different. The colour of the centre line indicated to the participant the condition (0-back: blue, 1-back: red; mean presentation duration=1050ms, 200ms jitter). The condition at the beginning of each session was counterbalanced across participants. Non-target trials were presented in runs of 2-8 trials (mean = 5) following which a target trial or multidimensional experience sampling (MDES) probe was presented.

During target trials, participants were required to make a behavioural response on the location of a specific shape. In the 0-back condition, on target trials, a pair of shapes were presented (as in the non-target trials), but the shapes were blue. Additionally, there was a small blue shape in the centre of the line down the middle of the screen. Participants were required to press a button to indicate which of the large shapes matched the central shape. This allowed participants to make perceptually-guided decisions so that this condition does not require continuous monitoring. In the 1-back condition, the target trial consisted of two red question marks either side of the central line (in place of the shapes). There was a small shape in the centre of the screen as in the 0-back condition, but it was red. Participants had to indicate via button press which of the two shapes from the previous trial the central shape matched. Therefore, the decisions in this condition were guided by memory and this part of the task required constant monitoring in case each non-target trial had to be used to guide this decision.

The contents of ongoing thought during this paradigm was measured using MDES. MDES probes occurred instead of a target trial on a quasi-random basis. When a probe occurred the participants were asked how much their thoughts were focused on the task, followed by 12 randomly shuffled questions about their thoughts (see

Table 1). The task was changed part way through data collection: for the first cohort (164 participants), participants answered on a sliding scale from 0 to 1, which was altered to a scale from 1 to 4 for 35 participants. This was due to the fact that the 35 participants were collected as control participants in a study (Martinon, Riby, et al., 2019) that also involved task performance inside the scanner. The task was altered to match the necessary use of a four-button box during scanning. There were no other changes to the task design. All scores were normalised to the same scale prior to principal component analysis (PCA). PCA decomposition on the 164 and 35 participants separately produced similar factors as shown by highly correlated question loadings (detail: $r(11)=.577$; off-task: $r(11)=.868$; modality: $r(11)=.944$; emotion: $r(11)=.838$). This matches previous work that showed highly similar dimensions of thought across conditions (A Turnbull et al., 2019) suggesting minimal effect of changing scale.

Dimensions	Questions	Low	High
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
Detailed	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

Table 1. Mind wandering questions asked to each participant during MDES. The first question was always "Task" then the other 12 questions in a random order. The scores from these questions were entered into a PCA.

The task was performed on three separate days in sessions that lasted around 25 minutes, and these were separated into eight blocks. In total, an average of 37.86 MDES probes occurred (SD=9.47). The answers to these questions were used to identify components of thought that demonstrated a consistent structure across

participants. The responses were concatenated into a single matrix and entered into a PCA with varimax rotation in SPSS (Version 25) to ensure maximally distinct components. Four components were selected based on the scree plot (see Figure 1), and to enable consistent interpretation with previous studies using this technique (C. Murphy et al., 2018; Sormaz et al., 2018; Adam Turnbull et al., 2019; Vatansever et al., 2018). These components were labelled (in order of decreasing eigenvalues) based on their question loadings: Detail, Off-task, Modality, and Emotion. The loadings for these components can be seen in Table 2. Where these are represented in wordclouds, the size of the word represents the loading score and the colour the direction (blue: negative, red:positive).

Question	PC1	PC2	PC3	PC4
Task	0.305	-0.711	-0.053	0.241
Future	0.383	0.596	-0.048	0.169
Past	0.419	0.335	0.120	-0.442
Self	0.280	0.703	0.019	0.105
Person	0.134	0.757	0.185	0.028
Emotion	0.193	0.102	0.127	0.861
Words	0.267	-0.090	-0.816	-0.002
Images	0.328	0.131	0.764	0.096
Evolving	0.651	0.108	0.002	0.017
Habit	0.606	0.090	-0.154	0.052
Detailed	0.729	-0.197	0.028	0.097
Vivid	0.665	0.167	0.310	0.036
Deliberate	0.429	-0.628	-0.187	0.104

Table 2. Loadings for each question from Table 1 on the four components of thought. Component 1 is largely defined by vividness and detail, component 2 by a negative relationship to task focus and positive person and self-related thought. Component 3 loads negatively on thinking in words and positively on thinking in images, while component 4 is predominantly indicative of a positive emotional valence.

5.3.3 Assessment of Autistic Traits and Symptoms

To assess ASD symptoms in this neurotypical population we administered the Autism Quotient (AQ) questionnaire (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001). This scale includes 50 questions divided across five subscales that measure traits associated with ASD diagnosis: social skills, attention switching,

attention to detail, communication, and imagination. Each subscale is scored out of 10 with increasing scores indicating higher ASD traits. The total score (out of 50) is derived by summing each of the five subscales, and a cut-off of 32+ was initially determined as optimal for discrimination of ASD individuals from neurotypical participants like those in our study. It was designed to quantify ASD traits in both individuals with and without an ASD diagnosis and was shown to have good test-retest and interrater reliability in both autistic and neurotypical populations (Baron-Cohen et al., 2001), making it an appropriate scale for the purposes of this neurotypical study. It has additionally been shown to correlate moderately to highly with the Social Responsiveness Scale, a well-established, published screening measure of autism (K. Armstrong & Iarocci, 2013; Bölte, 2012). A study comparing the AQ to the Autism Diagnosis Observation Schedule-Generic (ADOS-G) and Autism Diagnostic Interview-Revised (ADI-R), two gold-standard diagnostic clinical assessments of Autism found that the AQ had a high sensitivity and positive predictive value combined with a low specificity and negative predictive value (Ashwood et al., 2016). This means that the scale generally identifies autistic individuals by their high score on this measure (correct positives), but also misses a large portion of autistic individuals who score below the cut-off (false negatives). Taken together, these findings suggest that, while the AQ is useful in measuring ASD symptoms, it has limited use as a diagnostic tool and the cut-off scores are relatively poor indicators of an ASD diagnosis. In our sample, there was a mean AQ total score of 12.48 (S.D.=6.40), suggesting relatively low levels of autistic traits but with significant variation. The means for each subscale were as follows: AQ social (M=1.52, S.D.=1.94), AQ attention switching (M=3.46, S.D.=2.02), AQ attention to detail (M=3.77, S.D.=2.11), AQ communication (M=1.90, S.D.=1.93), AQ imagination (M=1.82, S.D.=1.87). Histograms showing the distribution of the AQ and its subscales can be seen in Supplementary Figure 2. Two participants scored over 32 (36 and 40), suggesting they were above the cut-off for this non-clinical scale. Additionally, several studies have found specific relationships between different subscales of the AQ and performance on a range of neurocognitive measures, suggesting that while they measure related traits that contribute to autism, they can be dissociated to understand links between different aspects of autism and neurocognitive processes (English, Maybery, & Visser, 2015; Fugard et al., 2011; Laycock, Cross, Dalle Nogare, & Crewther, 2014; Russell-Smith, Maybery, Bayliss, & Sng, 2012).

5.3.4 MRI Data Acquisition

All MRI scanning was carried out at the York Neuroimaging Centre. Structural and functional data were acquired using a 3T GE HDx Excite MRI scanner with an eight-channel phased array head coil tuned to 127.4 MHz. Structural MRI acquisition was based on a T1-weighted 3D fast spoiled gradient echo sequence (TR=7.8s, TE=minimum full, flip angle=20º, matrix size=256x256, 176 slices, voxel size =1.13x1.13x1mm). Functional data were recorded using single-shot 2D gradient echo planar imaging (TR=3s, TE=minimum full, flip angle=90º, matrix size=64x64, 60 slices, voxel size=3mm isotropic, 180 volumes). Participants completed a 9-minute eyes-open resting state scan during which there was a fixation cross on-screen. Participants were verbally instructed to look at the fixation cross and try to stay awake.

5.3.5 Data Pre-processing: Behavioural Data

All scores that were identified as outliers using SPSS (Version 25: quartile ± 1.5*interquartile range) were replaced by the median for further analyses to ensure the results were not driven by a small number of extreme values (Orr, Sackett, & Dubois, 1991). The use of 1.5*interquartile range is the default setting in SPSS and the use of this measure is preferable as the mean and standard deviation are greatly affected by outliers (Leys, Ley, Klein, Bernard, & Licata, 2013). The median is similarly considered a preferable imputation measure as it is unaffected by a few extreme values (Cousineau & Chartier, 2010). There were two participants who were replaced with the median for the Social subscale of the AQ. Three participants were replaced with the median for mean off-task thought and two were replaced for mean emotion of thought. Two were replaced for difference between tasks in detailed thought, and seven for modality difference. Inverse efficiency score was calculated by dividing mean reaction time by accuracy (percentage correct trials/100: equivalent to 1 minus the proportion of errors). Four participants were replaced with the median for inverse efficiency during the 0-back, and nine participants were outliers during the 1-back. All data were z-scored prior to correlational analyses. No part of the study analyses was preregistered prior to the research being conducted.

5.3.6 Data Pre-processing: Cortical Thickness

The extraction of cortical thickness followed the procedure in previous studies (X. Wang et al., 2018). FreeSurfer was used to estimate vertex-wise cortical thickness

(5.3.0; https://surfer.nmr.mgh.harvard.edu), using an automated surface reconstruction scheme described in detail elsewhere (Dale et al., 1999; Fischl & Dale, 2000; Fischl et al., 2001; Fischl et al., 1999). The following processing steps were applied: intensity normalisation, removal of non-brain tissue, tissue classification and surface extraction. Cortical surfaces were visually inspected and corrected if necessary. Cortical thickness was calculated as the closest distance between the grey/white matter boundary and pial surface at each vertex across the entire cortex. A surface-based smoothing with a full-width at half maximum (FWHM) = 20 mm was applied. Surface alignment based on curvature to an average spherical representation, fsaverage5, was used to improve correspondence of measurement locations among subjects.

5.3.7 Data Pre-processing: Resting State fMRI

Preprocessing of the resting state fMRI data was carried out using the SPM software package (SPM Version 12.0, http://www.fil.ion.ucl.ac.uk/spm/) based on the MATLAB platform (Version 16.a, https://uk.mathworks.com/products/matlab.html). The individual subject analysis first involved motion correction with six degrees of freedom and slice-timing correction. Structural images were coregistered to the mean functional image via rigid-body transformation, segmented into grey/white matter and cerebrospinal fluid probability maps, and images were spatially normalized to the MNI-152 template. Functional images were spatially smoothed using an 8mm Gaussian kernel. Due to the additional problems associated with motion in functional connectivity analyses (Power et al., 2012); additional denoising procedures were carried out using the CONN functional connectivity toolbox (Version 17.f, https://www.nitrc.org/projects/conn(Whitfield-Gabrieli & Nieto-Castanon, 2012)). An extensive motion correction procedure was carried out, comparable to that previously reported in the literature (Ciric et al., 2017). In additional to the removal of six realignment parameters and their second-order derivatives using a GLM (Friston et al., 1996), a linear detrending term was applied as well as the CompCor method with five principle components to remove signal from white matter and cerebrospinal fluid (Behzadi et al., 2007). Volumes affected by motion were identified and scrubbed if motion exceeded 0.5mm or global signal changes were larger than z=3. Nine participants that had more than 15% of their data affected by motion were excluded from the analysis (Power et al., 2014), and three additional participants were excluded

for problems associated with fMRI scanning. Global signal regression was not used in this analysis due to its tendency to induce spurious anti-correlations (K. Murphy et al., 2009; Saad et al., 2012). A band-pass filter was used with thresholds of 0.009 and 0.08Hz to focus on low frequency fluctuations (M. D. Fox et al., 2005).

5.3.8 Statistical Analysis: Behavioural Data

We first performed an analysis to investigate the relationship between thought components and task performance, to better understand the relationship between ongoing thought and the task context. We conducted a repeated measures ANOVA in which the average of the four components of thought, and the difference between these thoughts across the two tasks were included as covariates of interest. This was used to understand whether there was any relationship between the levels of thoughts in general and task performance, as well as interactions across the two tasks (types of thought that might be beneficial or detrimental only in one task). The difference scores were included to understand whether flexibility (regulating thought in line with task demands) was related to task performance, as well as to match models exploring relationships to autistic traits (see below). The dependent variable was IES that was calculated as reaction time over accuracy (meaning lower scores equate to better task performance), with the tasks as the two levels. Bivariate correlations were used to further elaborate any significant effects.

To assess relationships between the level of thoughts during experience sampling and autistic traits in our neurotypical participants, a repeated measures analysis of variance (ANOVA) was carried out. This was due to the large amount of dependence between the five subscales that are designed to measure related co-varying attributes. This included the five AQ subscales as levels of the dependent variable, and the mean scores for each component of thought, as well as their difference scores (mean 0-back minus mean 1-back) as covariates of interest. In this analysis, any between-subject effects can be interpreted as a relationship between that specific covariate and the mean (or total) of the five subscales. Effects that significantly differentiate between the subscales of the AQ would emerge as within-subject effects that could be more specifically probed using follow-up analyses. This method was chosen due to the exploratory nature of our study, in which we have no specific hypotheses and therefore aimed to describe the relationship with autistic traits

in general while allowing for the possibility of detecting subscale specific effects. A multivariate ANOVA, on the other hand, would only be able to find relationships to the specific subscales. Bivariate correlations were used to further elaborate any significant effects. Analyses were performed in SPSS (Version 25), and figures were made using the Matplotlib (Hunter, 2007) package in Python (Version 3.6.5). The data can be found at: https://github.com/adamgeorgeturnbull/autism.

5.3.8 Statistical Analysis: Cortical Thickness

Two separate models were created to assess the relationship between the AQ and whole-brain cortical thickness. As with the behavioural analysis, these were used to assess association with AQ total, as well as any specific relationships to the subscales. The first model included the total AQ score as a covariate of interest in a general linear model predicting cortical thickness on a voxelwise basis. The second model was identical to the first, but instead including all five subscales as covariates of interest within the same model. Age and gender were included as covariates of no interest. All results were corrected with a FWE cluster correction at p<.05 and a voxelwise threshold of p<.001. Significant clusters are described in Supplementary Table 1. Brain images in figures are made using BrainNet Viewer (Xia et al., 2013).

5.3.9 Statistical Analysis: Functional Connectivity

The peak of the significant result from the cortical thickness analysis was used to create a sphere (radius 6mm) using FSL (version 5). This was entered into a seed-based connectivity analysis using the CONN functional connectivity toolbox (Version 17.f, https://www.nitrc.org/projects/conn (Whitfield-Gabrieli & Nieto-Castanon, 2012)). In the same way as in the previous analyses, two models were set up: the first using the five subscales as the covariates of interest, and the second using the total score from the AQ. Mean motion (calculated in CONN), was included as a covariate of no interest. The results were corrected with a FWE cluster correction at p<.05 and a voxelwise threshold of p<.001 (Eklund et al., 2016). Significant clusters are described in Supplementary Table 2. The conditions of the European Research Council grant that funded this research do not permit public archiving of individual raw or processed MRI data. There are no conditions by which external researchers who do not have professional access to the York Neuroimaging Centre can access the individual level

raw or processed MRI data. The unthresholded images for the functional connectivity analyses can be found at https://neurovault.org/collections/5347/.

5.4 Results

5.4.1 Behavioural

5.4.1.1 Dimensions of Thought

We first applied Principal Component Analysis to the trial level experience sampling data to identify the patterns of covariance captured in our laboratory session. This identified four components of thought (see Scree plot in Figure 1). From their loadings on each of the questions (displayed as wordclouds in the upper panel of Figure 2) these were labelled as Detail, Off-task, Modality, and Emotion. These scores were averaged within each task (0-back, 1-back) to give a mean score per participant per task. Prior to performing t-tests, three participants' off-task scores in the 0-back were identified as outliers and replaced with the median, as were two participants' emotion scores in the 0-back and one in the 1-back. Paired t-tests revealed significant effects of task on each of the four components of thought. Participants engaged in significantly more Detailed thought in the 1-back condition (t(198)=-7.378, p<.001), and more Off-task thought in the 0-back condition (t(198)=10.027, p<.001). Additionally, participants thought more in images in the 0-back, and more in words in 1-back (t(198)=4.669, p<.001). Participants also had significantly more positive thoughts in the 1-back (t(198)=-2.146, p=.033). These results are summarised in the lower panel of Figure 2.
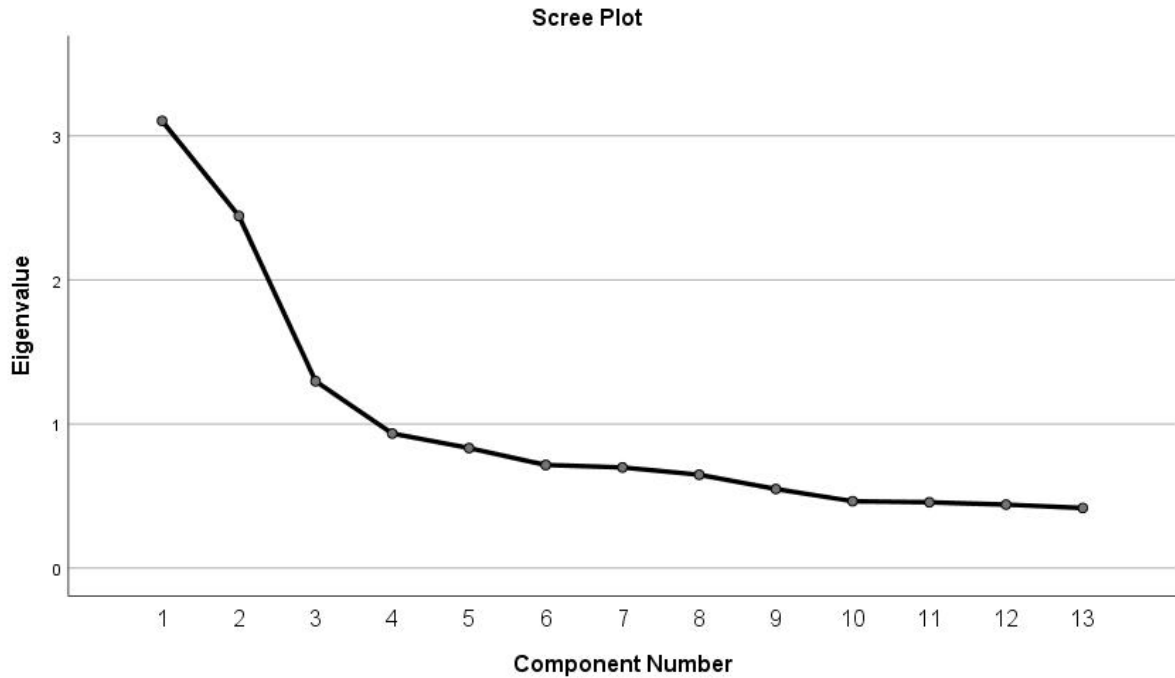
Figure 1. Scree plots showing the eigenvalues of the 4 components of thought following a PCA analysis of the 13 MDES question responses. The change in slope following component 4 was used to select 4 components for further analyses.
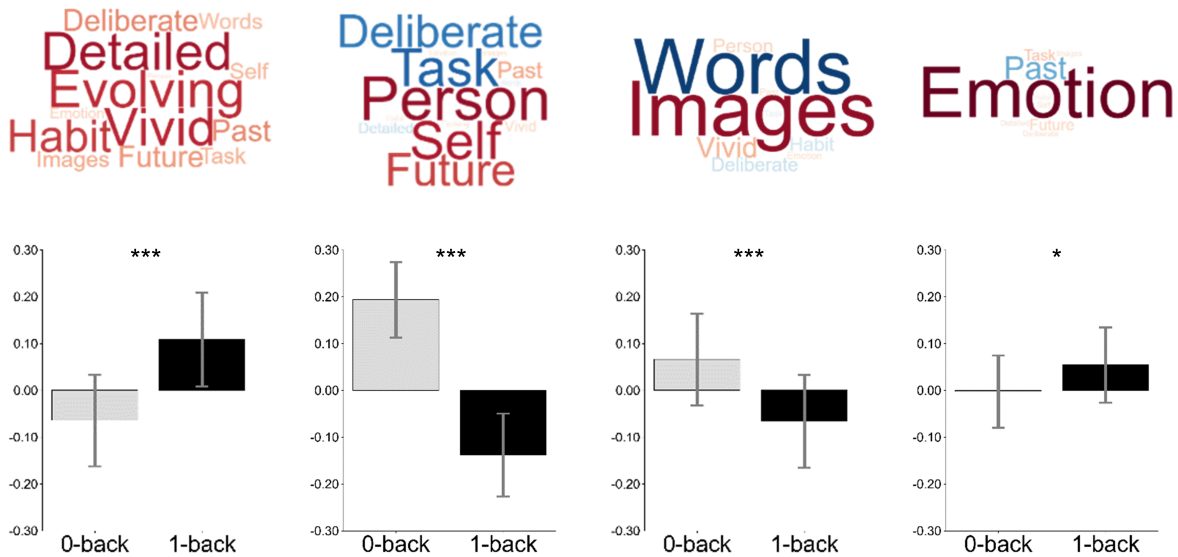
Figure 2. Distribution of thought patterns across tasks. A principal component analysis on the 13 questions asked at each occurrence of an MDES probe revealed four components. These were labelled: Detail, Off-task, Modality, and Emotion, based on the question loadings represented by the wordclouds. The size of the words indicates the magnitude of the loading for that question on each component, with the colour indicating the direction (red is positive, blue is negative). The mean levels of each type of thought in the easy task (0-back) and hard task (1-back) are represented in the bar charts, with error bars representing 95% confidence intervals.

5.4.1.2 Relationship with Task Performance

To better characterise the meaning of the patterns of thought, we examined their relationship to task performance (Figure 3, top). We conducted a repeated measures ANOVA in which the average of the four dimensions, and the task difference were included as covariates of interest, in a similar way to the model investigating autistic traits. The dependent variable was IES, with the tasks as the two levels. This revealed a main effect of task ($F(1,189)=272.777$, $p<.001$) indicating that performance was more efficient in the 0-back task (mean=0.844, S.D.=0.206) than in the 1-back task (mean=1.069, S.D.=0.246). There were no interactions between task and mean Detail ($F(1,189)=0.231$, $p=.631$), mean Modality ($F(1,189)=3.661$, $p=.057$), or mean Emotion ($F(1,189)=1.331$, $p=.250$). Nor were there any significant interactions between task and any of the thought task differences (Detail: $F(1,189)=1.142$, $p=.287$; Off-task: $F(1,189)=0.039$, $p=.843$; Modality: ($F(1,189)=0.853$, $p=.357$; Emotion: $F(1,189)=2.601$, $p=.108$). There was a significant interaction between task and mean Off-task thought ($F(1,189)=5.033$, $p=.026$). There was also a significant between subjects effect for mean Modality ($F(1,189)=3.969$, $p=.048$). Finally, there were no other between subject effects for either mean thought levels (Detail: $F(1,189)=3.105$, $p=.080$; Off-task: $F(1,189)=0.188$, $p=.665$; Emotion: $F(1,189)=0.005$, $p=.810$) and no significant effect of the differences in thought levels between the tasks (Detail: $F(1,189)=0.952$, $p=.330$; Off-task: $F(1,189)=0.223$, $p=.637$; Modality($F(1,189)=0.855$, $p=.356$; Emotion: $F(1,189)=0.292$, $p=.590$). The within-subject effects can be seen in Table 3 and the between-subject effects can be seen in Table 4.

Within-subjects effects	Type III Sum of Squares	df	Mean Square	F	Sig.
Task	5.046	1	5.046	272.777	.000
Task * mean detail	.004	1	.004	.231	.631
Task * mean off-task	.093	1	.093	5.033	.026
Task * mean modality	.068	1	.068	3.661	.057
Task * mean detail	.025	1	.025	1.331	.250
Task * detail difference	.021	1	.021	1.142	.287
Task * off-task difference	.001	1	.001	.039	.843
Task * modality difference	.016	1	.016	.853	.357
Task * emotion difference	.048	1	.048	2.601	.108
Error(task)	3.496	189	.018		

Table 3. Within-subject effects for a repeated measures ANOVA looking at the relationship between task performance measured by inverse efficiency and dimensions of thought. This table represents interactions between efficiency in each task condition and levels of thought. Mean levels of thought as well as the difference between the two tasks are included to look at links between types of thinking in general and context-dependent flexibility in types of thinking. There was a significant interaction between task condition and off-task thinking.

Between-subjects effects	Type III Sum of Squares	df	Mean Square	F	Sig.
Intercept	362.344	1	362.344	4393.720	.000
Mean detail	.256	1	.256	3.105	.080
Mean off-task	.016	1	.016	.188	.665
Mean modality	.327	1	.327	3.969	.048
Mean emotion	.005	1	.005	.058	.810
Detail difference	.079	1	.079	.953	.330
Off-task difference	.018	1	.018	.223	.637
Modality difference	.071	1	.071	.855	.356
Emotion difference	.024	1	.024	.292	.590
Error	15.587	189	.082		

Table 4. Between-subject effects for a repeated measures ANOVA looking at the relationship between task performance measured by inverse efficiency and dimensions of thought. This table represents overall effects between mean efficiency and levels of thought. Mean levels of thought as well as the difference between the two tasks are included to look at links between types of thinking in general and context-dependent flexibility in types of thinking. There was a significant relationship between efficiency and modality of thought.

To follow up these analyses, we extracted parameter estimates from the model to understand the direction of these results. There was a positive relationship between mean Modality and IES in the 1-back (B=.043) that was also positive but weaker in the 0-back (B=.016). To understand if this effect was driven by thinking in images vs. words in each task specifically, we performed bivariate correlations. The relationship was significant for modality during the 1-back and IES in the 1-back (r(197)=.233, p=.001) but not IES during the 0-back task (r(197)=.102, p=.153). There was no relationship between Modality in the 0-back and IES in either task (0-back: r(197)=.048, p=.504; 1-back: r(197)=.127, p=.073). Together these results suggest that thinking more in words during the 1-back task was generally associated with more efficient task performance in this paradigm. In contrast, we found that off-task thought during the 1-back specifically was detrimental to performance as measured by IES in

the 1-back (r(197)=.148, p=.037) but not the 0-back task (r(197)=.045, p=.526), while off-task thought in the 0-back was not associated with task performance in either task (0-back: r(197)=-.059, p=.408; 1-back: r(197)=.037, p=.599).

Together these analyses show that during the 1-back task participants tended to describe their thoughts as having greater detail, more related to the task, more in the form of words, and more positive in emotional tone. Moreover, greater on-task thought and the use of words were related to better performance during the 1-back task specifically.

5.4.1.3 Relationship with Autistic Traits in Neurotypical Individuals

Our next analysis examined whether the experience individuals reported during the task was associated with the variance in autistic traits across the sample (Figure 3, bottom). We performed a repeated measures ANOVA in which the mean levels of thought, as well as the difference between the tasks, were included as explanatory variables (a total of 8 scores) and the five subscales of the AQ were included as dependent variables. The within-subject effects can be seen in Table 5 and the between subject effects can be seen in Table 6.

Within-subject effects	Type III Sum of Squares	df	Mean Square	F	Sig.
AQ subscale	811.531	4	202.883	68.525	.000
AQ subscale * mean detail	6.927	4	1.732	.585	.674
AQ subscale * mean off-task	5.695	4	1.424	.481	.750
AQ subscale * mean modality	6.936	4	1.734	.586	.673
AQ subscale * mean emotion	7.781	4	1.945	.657	.622
AQ subscale * detail difference	6.761	4	1.690	.571	.684
AQ subscale * off-task difference	8.994	4	2.249	.759	.552
AQ subscale * modality difference	3.499	4	.875	.295	.881
AQ subscale * emotion difference	6.190	4	1.547	.523	.719
Error(AQ subscale)	2036.970	688	2.961		

Table 5. Within-subject effects for a repeated measures ANOVA looking at the relationship between AQ subscale and dimensions of thought. This table represents interactions between AQ subscale and levels of thought. Mean levels of thought as well as the difference between the two tasks are included to look at links between types of thinking in general and context-dependent flexibility in types of thinking. There were no significant effects.

Between-subjects effects	Type III Sum of Squares	df	Mean Square	F	Sig.
Intercept	5554.501	1	5554.501	759.141	.000
Mean detail	7.959	1	7.959	1.088	.298
Mean off-task	6.618	1	6.618	.904	.343
Mean modality	49.341	1	49.341	6.744	.010
Mean emotion	.015	1	.015	.002	.964
Detail difference	.044	1	.044	.006	.938
Off-task difference	.647	1	.647	.088	.767
Modality difference	.282	1	.282	.039	.845
Emotion difference	4.129	1	4.129	.564	.454
Error	1258.494	172	7.317		

Table 6. Between-subject effects for a repeated measures ANOVA looking at the relationship between AQ subscale and dimensions of thought. This table represents overall effects between AQ mean (or total) and levels of thought. Mean levels of thought as well as the difference between the two tasks are included to look at links between types of thinking in general and context-dependent flexibility in types of thinking. Mean modality was significantly related to total AQ score.

The results of this analysis revealed a significant between-subjects effect of mean levels of Modality ($F(1,170)=6.744$, $p=.010$), indicating a significant relationship with overall autistic traits (see Table 6). There were no significant between-subject effects of the mean levels of the other components (Detail: ($F(1,170)=1.088$, $p=.298$; Off-task: ($F(1,170)=0.904$, $p=.434$; Emotion: ($F(1,170)=0.002$, $p=.964$). There were also no significant between-subjects effects of the difference between levels of thought in the two tasks on autistic traits (Detail: ($F(1,170)=0.006$, $p=.938$; Off-task: ($F(1,170)=0.088$, $p=.767$; Modality: $F(1,170)=0.039$, $p=.845$; Emotion: ($F(1,170)=0.564$, $p=.454$). There were no significant within-subjects effects related to the thoughts (no interactions between the thoughts and the specific AQ subscales, see Table 5).

To further understand the meaning of the relationship between Modality and total autistic traits, we performed post-hoc bivariate correlations between mean Modality and total AQ score, as well as the Modality scores separately in each task. These results are summarised in Figure 3 (bottom). These correlations showed a negative relationship between total AQ score and Modality ($r(179)=-.198$), and this was significant in both tasks (0-back ($r(179)=-.206$, $p=.005$),1-back ($r(179)=-.175$, $p=.019$)). This indicates that higher levels of autistic traits were linked to thinking more in words in both task conditions.

Finally, since thinking in words was associated with both better performance, and higher autistic traits, we conducted a further exploratory analysis to determine whether autistic traits were related to better performance. We calculated the correlations between AQ total score and task performance, and found no relationship in either task (0-back: $r(179)=-.066$, $p=.381$; 1-back: $r(179)=-.046$, $p=.541$). This suggests that, while overall autistic traits and task performance are both related to thinking in words, there is no reliable direct relationship between autistic traits and task performance in this neurotypical sample.
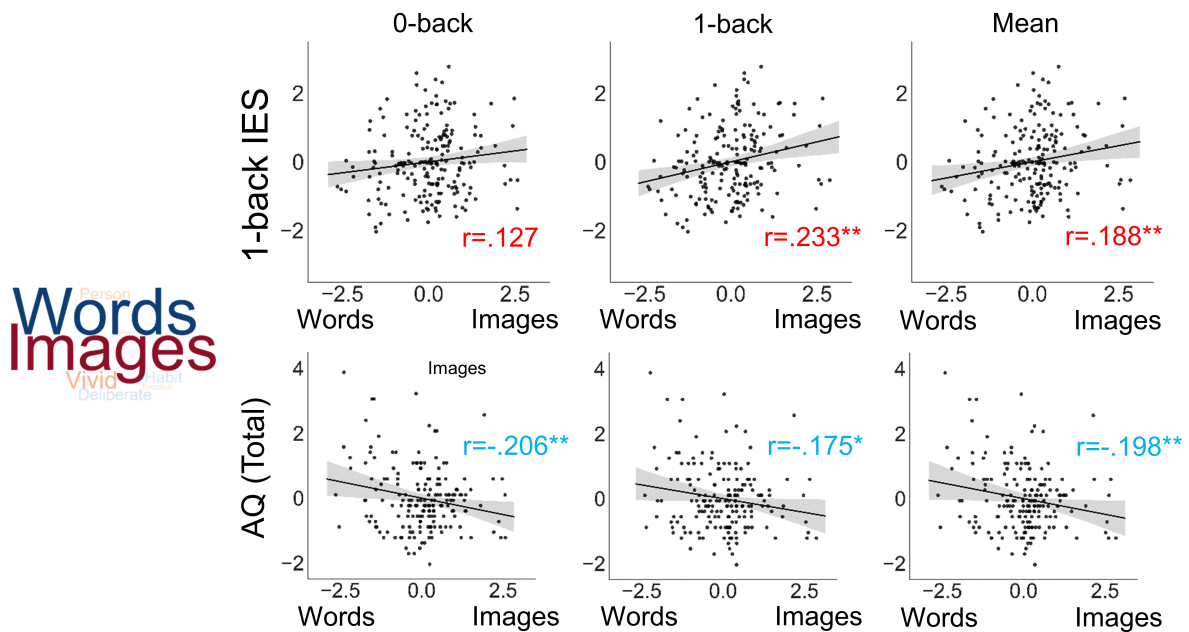
Figure 3. Descriptions of thoughts in the form of words is related to task performance and autistic traits. Modality of thought during 1-back performance, but not 0-back performance, is significantly related to inverse efficiency in both the 0 and 1-back tasks. Mean modality of thought is also related to the total score on the AQ, with thinking in words significantly related to more autistic traits. This relationship holds across both tasks. The question loadings that make up "Modality" are represented by the wordcloud, showing that this component is made up of a large positive loading on thinking in images and a large negative loading on thinking in words.

5.4.2 Neural Analysis

5.4.2.1 Cortical Thickness

Our first exploratory neural analysis examined whether there was an overall relationship between autistic traits and whole-brain cortical thickness in a neurotypical sample. To do so we performed two GLM analyses (both including age and gender as covariates of no interest), one to detect overall relationships to the total AQ score, and another to detect specific relationships to each of the specific subscales. There were no significant effects of AQ total score on cortical thickness that passed whole brain correction (FWE cluster correction at $p<.05$ and voxelwise $p<.001$). In our second model there was a significant effect of AQ social skills, which revealed a cluster in the left lingual gyrus (LG) in which mean cortical thickness increased with the social skill component of the AQ (left side of Figure 4: increased score is related to greater difficulties in social skill/motivation). Notably, cortical thickness within the LG has been linked to autism in prior studies using clinically defined samples (Cauda et al., 2011). The specific location and size of this result is summarised in Supplementary Table 1.

5.4.2.2 Functional Connectivity

Having determined a region linked to variation in social deficits associated with autism, we next explored its functional connectivity and whether it varied with population variation in autistic traits. First, we performed a resting state connectivity analysis with motion as a covariate, and used the unthresholded result to perform a meta-analytic decoding using Neurosynth (Yarkoni et al., 2011). As well as expected terms such as "Visual", this region also appeared to relate to motor performance, as well as speech production (captured by "Speech" as well as "Vocal").

Next, we examined whether this region's functional behaviour was linked to autistic traits in two exploratory models. These models were set up in a similar way as for cortical thickness: one with total AQ score and one with all five subscales. For the analysis of overall levels of autism this model identified two clusters in motor cortex with stronger functional coupling for individuals who were higher on overall scores on the AQ (see Figure 4). Performing a meta-analytic decoding of these regions using Neurosynth, identified similar terms including "speech" as well as action related words such as "execution", "coordination", as well as "motor imagery". Our second analysis identified that stronger functional connectivity between the LG and two clusters in ventral medial prefrontal cortex (vMPFC) and medial superior parietal lobule (mSPL) was related to problems in the imagination subscale of the AQ (see Figure 5). Neurosynth decoding of these results highlighted terms linked to social processing ("theory of mind", "mentalizing" and "action observation") (Yarkoni et al., 2011). These results are summarised in Supplementary Table 2.
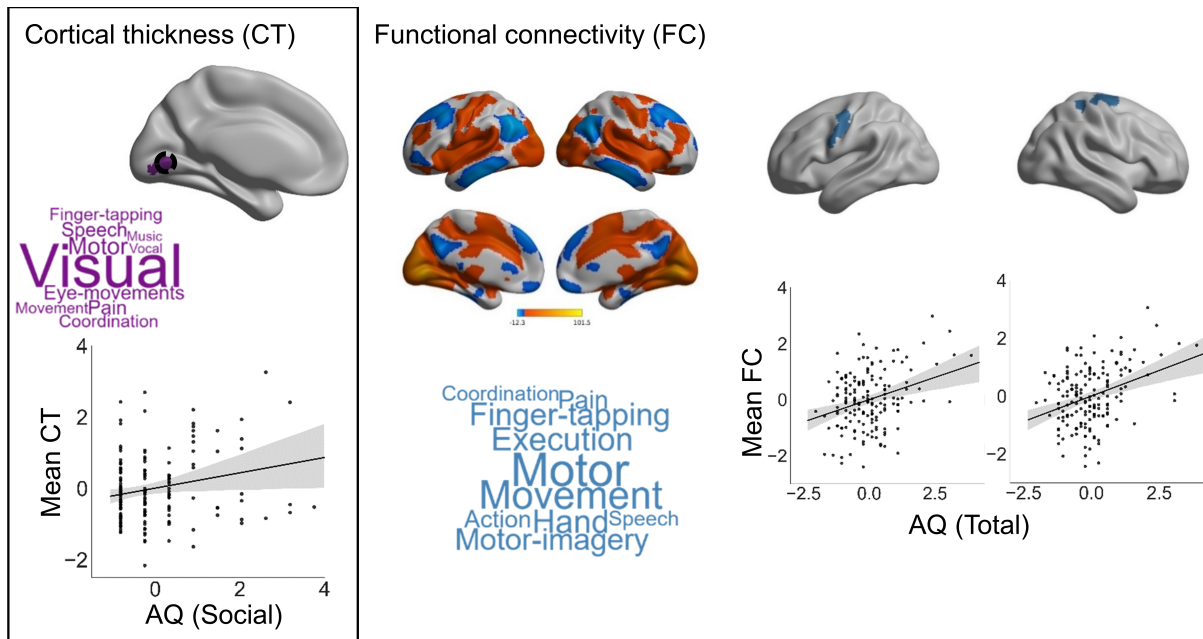
Figure 4. Cortical thickness in lingual gyrus (LG) and functional connectivity between this region and motor cortex are related to autistic traits. A cortical thickness analysis identified a region of left LG that was positively related to autistic social traits as measured by the AQ (left panel). Using the peak of this region as a seed, a functional connectivity analysis found that the strength of correlations between this seed and two clusters in bilateral regions of motor cortex is linked to general levels of autistic traits (right). A meta-analytic decoding of the relationship between AQ total score and functional connectivity from this seed identified sensorimotor terms that are represented in the wordcloud (bottom middle). The intrinsic functional connectivity of the left LG showed that it was related to sensorimotor networks (middle top). The results were corrected with a FWE cluster correction at p<.05 and a voxelwise threshold of p<.001.
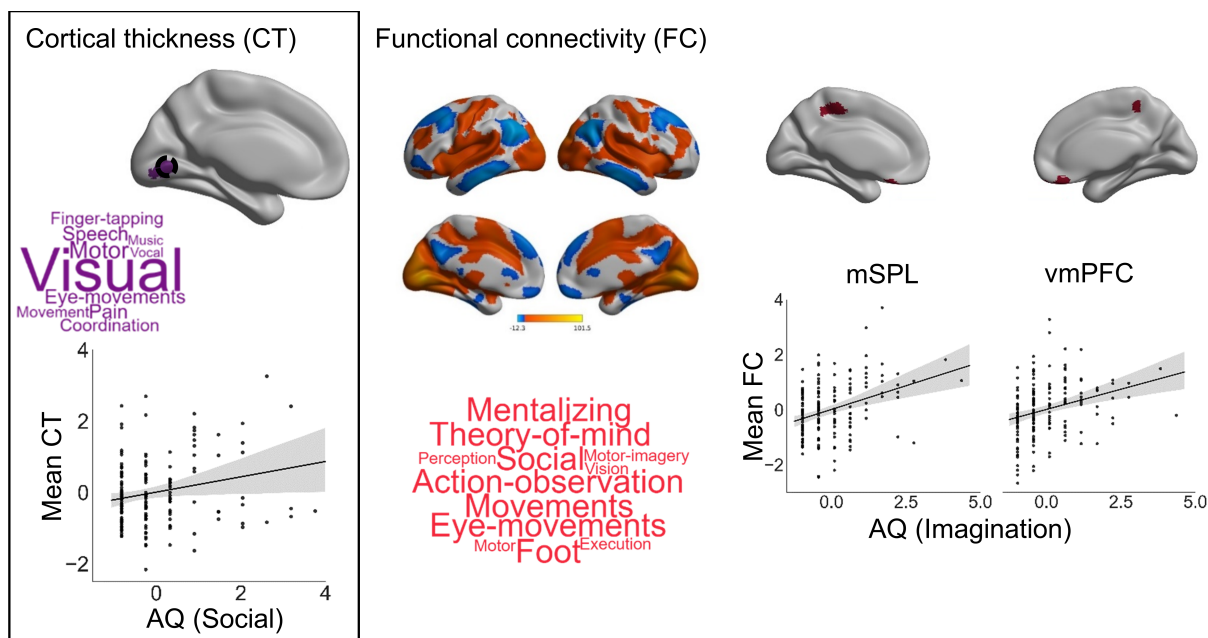
Figure 5. Functional connectivity between lingual gyrus (LG) and medial frontal and parietal regions are related to levels of deficit in imagination. Using the peak of the LG (left panel) as a seed, a functional connectivity analysis found that stronger correlation with clusters in ventromedial prefontal cortex and medial superior parietal lobule are linked to deficits in imagination linked to autism (right). A meta-analytic decoding of the relationship between AQ imagination score and functional connectivity from this seed identified terms related to social processing and action observation that are represented in the wordcloud (bottom middle). The intrinsic functional connectivity of the left LG showed that it was related to sensorimotor networks (middle top). The results were corrected with a FWE cluster correction at p<.05 and a voxelwise threshold of p<.001.

5.4.2.3 Relationship between Neural and Experiential Correlates of Autism

So far our analysis has identified correlates of autistic traits in neurotypical individuals in two domains: experiential (greater tendency to think in words) and neural (increased cortical thickness in the LG and greater connectivity between this region and motor cortex, as well as vMPFC/mSPL). Our final analysis explored whether these patterns of association captured common variance in autistic traits. Prior to these analyses, one participant's connectivity score to left motor cortex was determined an outlier and replaced with the median. We first performed simple bivariate correlations between all the variables of interest (see Supplementary Table 3). These revealed a significant negative relationship between mean Modality and FC between the left LG and left motor cortex (r(163)=-.212, p=.006) as well as a correlation between left LG FC to right motor cortex with the task difference in off-task thought (r(163)=.198,

p=.011). Additionally, a weak relationship was identified between cortical thickness in the left LG and the difference in modality between the 0-back and 1-back (r(163)=-.155, p=.046), indicating that greater cortical thickness was more strongly related to thinking more in words during the 0-back (where on average this type of thinking is less common).

The association with the modality of thought indicates that overall levels of autistic traits within our sample were linked to higher connectivity between the left LG and left motor cortex, and to thinking in words. To formally understand this relationship we conducted a univariate ANOVA in which total AQ score was the dependent variable and mean FC (left LG to left motor cortex), overall Modality of thought, and their interaction were predictors. In this model, Modality no longer significantly predicted AQ total score (F(1,161)=3.718, p=.056), but both FC (F(1,161)=9.456, p=.002) and the interaction between FC and Modality were significant (F(1,159)=8.486, p=.004). To visualise this effect we separately plotted the correlation between AQ and the modality component for individuals above and below the median FC score (see Figure 6). Bivariate correlations between the AQ total score and Modality were significant for the high FC group (r(81)=-.285, p=.009), but not for the low FC group (r(80)=-.058, p=.603, see Figure 6). This suggests that a significant part of the association between modality and autistic traits could be explained by the functional connectivity between the LG and the functional connectivity with motor cortex.

Relationship between AQ and images/words is moderated by FC
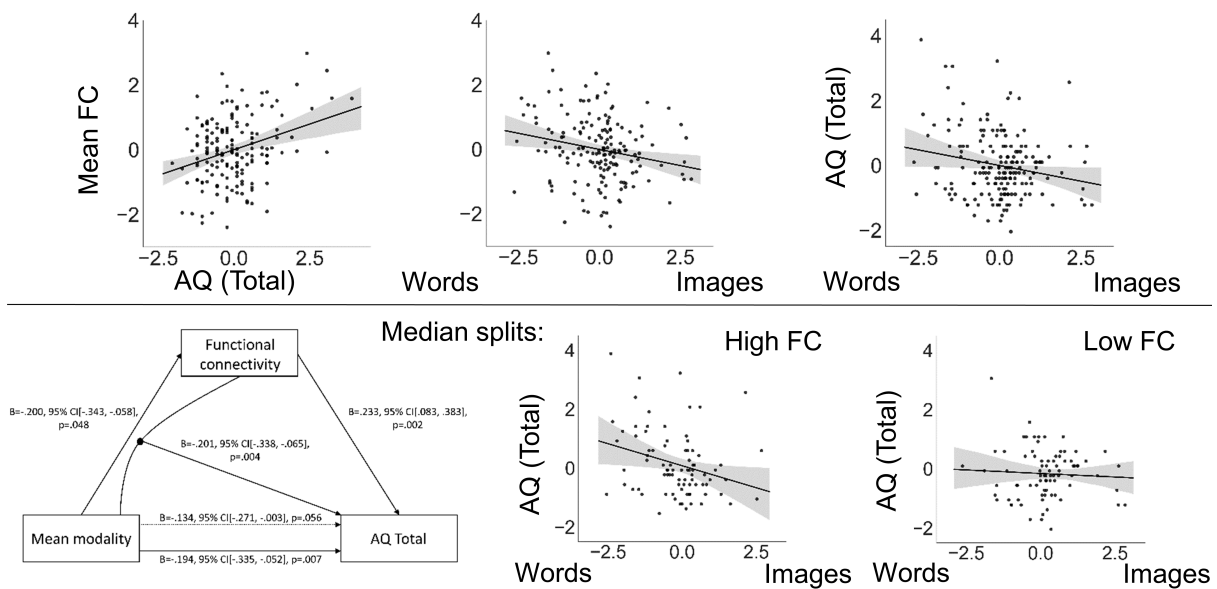
Figure 6. Functional connectivity between left LG and left motor cortex moderates the relationship between thinking in words and autistic traits. Autistic traits were found to be related to functional connectivity between the left LG and left motor cortex (top left) as well as thinking in words (top right). Additionally, the same functional connectivity was related to thinking in words (top middle). The relationship between thinking in words and autistic traits was explained by the functional connectivity between LG (bottom left). A median split based on functional connectivity (bottom right) shows that the relationship between thinking in words and autistic traits was only present for individuals with high functional connectivity between the left LG and left motor cortex.

5.5 Discussion

In this exploratory study, we found that autistic traits in a neurotypical population measured by the AQ were related to thinking more in words during the performance of a simple laboratory task. This effect was present in both easier and more difficult conditions, suggesting this pattern is not dependent on task context. In addition, we found that in general people thought more in words during the 1-back task, and this type of thought was found to be a beneficial strategy in the harder 1-back task when information has to be maintained in working memory. We also found that social deficits linked to autism were associated with greater cortical thickness in the LG and that the functional connectivity between this region and motor cortex was higher for individuals who were high on autistic traits generally. Importantly, the relationship between autistic traits and thinking in words was moderated by connectivity between a region of left LG and the left motor cortex: a link between autism and thinking in words was only observed for individuals with high connectivity between these two regions. Additionally, it was found that connectivity from the same region of left LG was related

to ASD-associated imagination difficulties, so that higher connectivity was linked to a greater difficulty in imagining as measured by the AQ.

Our study suggests that autistic traits in neurotypical individuals are associated with thinking more in words in a manner that is unaffected by task context. This pattern is not consistent with views of autism as linked to the excessive use of imagery or "thinking in pictures" (Kunda & Goel, 2011), however, it is consistent with finding that individuals with ASD use verbal strategies to mediate verbal short-term memory (D. M. Williams et al., 2012). It is important to keep in mind that our paradigm uses shapes and asks for a location decision, so it has important visual requirements. Two studies have used a similar n-back design in individuals with autism to understand verbal vs. visual processing, one using visually presented letters (Koshino et al., 2005) and one using faces (Koshino et al., 2007). While these studies present evidence for increased use of image-based processing, they found no behavioural differences. The interpretation of increased visual processing was made purely through reverse inference of differences in the networks recruited in fMRI data, which should be interpreted with caution (Poldrack, 2011). Our result of increased thinking in words adds to the complex literature on this topic (Kunda & Goel, 2011; D. Williams, Happé, & Jarrold, 2008; D. M. Williams et al., 2012; D. M. Williams & Jarrold, 2010), and further suggests that caution should be applied to interpreting "superficially similar behaviour" as indicating the underlying strategies (Kunda & Goel, 2011), when these processes can be relatively directly characterised using techniques such as MDES. Despite these points, it is still surprising that the relationship we identified was in the direction of increased thinking in words. While studies have challenged the idea that verbal strategies are deficient in autism (Kunda & Goel, 2011; D. M. Williams et al., 2012), there is little evidence to suggest that there is enhanced use of verbal processing associated with autistic traits. This result could also relate to the use of a neurotypical sample with low levels of autistic traits in the present study, however, the fact that several studies show enhanced visuospatial processing in relation to the AQ still makes it surprising in this sample (Fugard et al., 2011; Grinter et al., 2009). It may be that this result is specific to the use of simple verbal strategies to perform working memory tasks and does not generalise to overall experience in autistic individuals. Studies using experience sampling in different contexts, such as daily life, would help

to answer these questions, and it will be important to replicate these results in individuals with ASD diagnoses before any strong conclusions are drawn.

Beyond modality of thought, our results are also consistent with evidence that autistic traits may be associated with inflexibility in patterns of cognition. Our study shows that while modality of thought normally varies with task conditions in our paradigm, this flexible change was not reflected in the links to autistic traits observed in both conditions of our study. Increased word use in individuals with higher self-rated autistic traits independently of task condition suggests a pattern that is broadly consistent with the association between cognitive inflexibility and autism, compromising effective selection and deployment of appropriate cognitive strategy (Van Eylen et al., 2011).

At the neurobiological level, we extended prior observations of increased cortical thickness in the left LG in autistic individuals to found in meta-analyses of the literature (Cauda et al., 2011; Philip et al., 2012) to autistic traits in a neurotypical population. While this was found specifically related to social deficits, functional connectivity of this region to the motor cortex was related to autistic traits in general.

Since the LG is consistently found as both structurally and functionally different in ASD (Cauda et al., 2011; Philip et al., 2012), this highlights an important overlap between our neurotypical sample and prior studies with a more clinical focus. Notably, the location of the region of left LG that shows consistent deactivation to visual processing tasks in ASD (Philip et al., 2012) is very close in location to the region identified as related to social difficulties in our analysis (see Figure 7). Importantly, our analysis found that LG
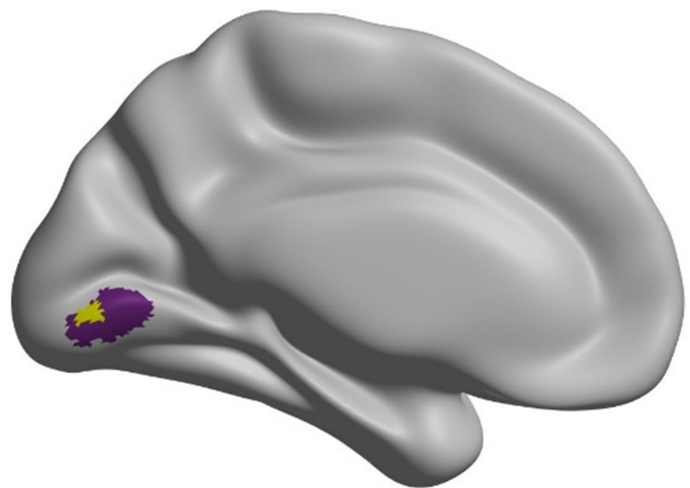
Figure 7. The region of left lingual gyrus (LG) linked to autistic social traits shows consistently different activation in clinical autistic populations. The cluster identified by our cortical thickness analysis (purple) is close to a region of left LG consistently found to show different activation in autistic individuals during visual processing tasks (yellow) (Philip et al., 2012).

to motor cortex connectivity explained the links between autism and thinking in words. In our neurotypical sample, only those in the high connectivity group showed the association between autistic traits and thinking in words. This pattern of results

suggests that the emphasis on the verbal modality in participants with higher autistic traits may be partly related to their underlying functional and structural neural architecture.

More generally, one important theme from our study is that the neural regions linked to autistic traits in neurotypical individuals tended to fall either within regions related to primary sensory processing (left LG and motor cortex) or regions related to higher order processing (vMPFC and mSPL). This is in broad agreement with evidence of aberrant brain processing in autism which often identifies changes in both unimodal (Bomba & Pang, 2004; Bruneau et al., 1999; Gaffrey et al., 2007; Gervais et al., 2004; Hyde et al., 2010; Mostofsky et al., 2007; Nebel et al., 2014; Théoret et al., 2005; Villalobos et al., 2005) and transmodal cortex (Di Martino, Ross, et al., 2009; Gotts et al., 2012; Hadjikhani et al., 2007; Kennedy & Courchesne, 2008a, 2008b; Lynch et al., 2013; Monk et al., 2009). It is possible that these types of deficit are related: a recent study highlighted differences in autism at both ends of a unimodal-transmodal continuum, and suggested that the normal segregation between these systems can breakdown in this condition (Hong et al., 2019). From our study, the increased connectivity within the sensorimotor system and the ventral medial pre-frontal cortex may reflect this absence of segregation. Problems segregating aspects of cortex important for higher order thought from those involved in acting and doing, may explain some of the features of autism since it could promote sensory processing (Adams & Jarrold, 2012), while impeding the decoupling of attention from external information that is thought to be important in processes such as theory-of-mind (Konishi et al., 2015; C. Murphy et al., 2018; Ruby, Smallwood, Sackur, et al., 2013; Sormaz et al., 2018). This could explain, for example, why autistic individuals struggle to imagine characters in books since this requires attention to go beyond the concrete visual information that makes up the words on the page, and why autistic individuals have difficulties imagining the intentions of people during social interaction, since this often depends on motives that extend beyond the moment.

While we have identified a relationship to task context that can be understood within models of autism as characterised by an inability to use context to flexibly adjust behaviour and thinking in line with the demands of the external environment (Vermeulen, 2015), it is important to note that we found no relationship to off-task thought itself. Participants seem to regulate levels of all four dimensions of thought

across the two task conditions, suggesting a relationship to the task for all four thought patterns. However, while we found some evidence of context-related inflexibility associated with modality, it is surprising that the dimension most clearly related to the task in both its loadings and size of modulation showed no such effect. This may simply be due to the fact that this neurotypical sample has a relatively low level of autistic traits, and these difficulties in cognitive flexibility are more apparent in autistic individuals. It is important to extend this type of experience sampling technique into clinical samples to allow us to understand the mappings between these data and more severe aspects of autistic symptomology. Alternatively, recent evidence has cast doubt on the idea that autism is characterised by cognitive inflexibility as measured experimentally (Geurts, Corbett, & Solomon, 2009). Interpreting our results with both this evidence and theories of contextual blindness in mind, it may be that the off-task component is more related to attention, a process that appears unchanged in autism (Sanders et al., 2008), than contextual dependent flexibility per se. Utilising contextual clues to adapt a beneficial task strategy, the process we believe may underlie the modality result, may require a more abstract contextual cueing that could be negatively related to autistic traits. Further research will be needed to fully unpack these clearly overlapping processes that are difficult to disentangle using the current approach.

5.5.1 Limitations

Although our study provides insights into the nature of the pattern of thoughts that are linked to autistic traits in a healthy population, it leaves many important questions unanswered. First, the use of a non-clinical sample of undergraduates, with a small age range and a large number of females makes comparison between these results and those in the wider autism literature difficult. There are some studies that suggest overlapping trends in neural circuitry in healthy individuals with higher levels of autistic traits as those in individuals diagnosed with ASD (Barttfeld et al., 2013; Di Martino, Shehzad, et al., 2009; Iidaka, Miyakoshi, Harada, & Nakai, 2012; Jakab et al., 2013), but this literature is relatively limited. Second, it is important to note that, while the AQ is a widely used measure of autistic symptoms that correlates with other published screening measures of ASD (K. Armstrong & Iarocci, 2013; Bölte, 2012), it does not have the sensitivity of gold-standard clinical assessments such as the ADOS-G or ADI-R (Ashwood et al., 2016). Additionally, the levels of autistic traits are low in our sample, meaning that several effects we find could be specific to this population.

Extending this research into clinical populations is essential before any conclusions can be drawn about these processes in autism.

Fourth, we used a cross-sectional approach in which we related intrinsic brain organisation to traits measured outside the scanner. This approach has identified links between brain connectivity and both autistic traits (Barttfeld et al., 2013; Di Martino, Shehzad, et al., 2009; Jakab et al., 2013) and spontaneous thought (Golchert et al., 2017; Gorgolewski et al., 2014; Medea et al., 2016; Poerio et al., 2017; Smallwood et al., 2016; Adam Turnbull et al., 2019; Vatansever et al., 2018; Villena-Gonzalez et al., 2018; H.-T. Wang, D. Bzdok, et al., 2018; H.-T. Wang, G. Poerio, et al., 2018). However, it is important to note that studies like the current one describe traits, rather than momentary states that often occupy our minds in daily life. Accordingly, it will be important in the future to examine associations between patterns of neural activity and momentary measures of experience in individuals with and without a formal diagnosis of ASD.

Fifth, we also found a pattern of increased connectivity to both the vMPFC and mSPL as associated with specific problems in imaginative deficits associated with autism. A cognitive decoding of this relationship suggests that the relationship between connectivity and imagination is driven by hyperconnectivity of the left LG to regions involved in social processing such as "action observation" and "theory of mind". There was no relationship between this pattern of connectivity and thinking during task performance, suggesting that this is not related to the changes in the modality of thought we found that was linked to autistic traits. It the future it will be important to understand whether these patterns of functional connectivity are related to specific behavioural or cognitive outcomes in autism.

Finally, our study is exploratory in nature, and several of the follow-up analyses are performed on the basis of the results of our initial findings. We have attempted to mitigate the negative consequences of this by performing models that include the same predictors across behavioural and neuroimaging modalities. However, this exploratory process is one that increases the likelihood of our findings being specific to this specific. While we believe the exploratory nature of this study was appropriate given the lack of studies using experience sampling and fMRI in relation to autistic

symptomology, it will be particularly important to replicate these findings using pre-specified, falsifiable research questions based on the results of the current study.

5.6 Conclusion

In conclusion, our analysis of a group of neurotypical undergraduates found that autistic traits were related to thinking in words during an alternating 0-back, 1-back task. Thinking in words was shown to be a successful strategy for task performance in the harder 1-back task, but analysis suggests this was driven by different variance to that linking this pattern of thoughts to autistic traits. Structural and functional correlates of autistic traits were identified in both sensorimotor regions (e.g. LG), and in transmodal regions (e.g. ventral mPFC). Importantly, connectivity between the left LG and left motor cortex was found to moderate the relationship between autistic traits and the modality of experience, suggesting a plausible biological basis for the tendency for neurotypical individuals with higher levels of autistic traits to think in words rather images.

Chapter 6 – Reductions in task positive neural systems occur with the passage of time and are associated with changes in ongoing thought

This chapter is adapted from: Turnbull, A., Karapanagiotidis, T., Wang, H. T., Bernhardt, B., Leech, R., Margulies, D., Schooler, J., Jefferies, E., & Smallwood, J. (2020). Reductions in task positive neural systems occur with the passage of time and are associated with changes in ongoing thought. *Scientific Reports* **(in press).**

6.1 Abstract

Cognition is dynamic and involves both the maintenance of and transitions between neurocognitive states. While recent research has identified some of the neural systems involved in sustaining task states, it is less well understood how intrinsic influences on cognition emerge over time. The current study uses fMRI and Multi-Dimensional Experience Sampling (MDES) to chart how cognition changes over time from moments in time when external attention was established. We found that the passage of time was associated with brain regions associated with external attention decreasing in activity over time. Comparing this pattern of activity to defined functional hierarchies of brain organization, we found that it could be best understood as movement away from systems involved in task performance. Moments where the participants described their thoughts as off-task showed a significant similarity to the task-negative end of the same hierarchy. Finally, the greater the similarity of a participant's neural dynamics to this hierarchy the faster their rate of increasing off-task thought over time. These findings suggest topographical changes in neural processing that emerge over time and those seen during off-task thought can both be understood as a common shift away from neural motifs seen during complex task performance.

6.2 Introduction

Cognitive states change with the passage of time, both in form and content (Welhaf et al., 2019). In recent years, neuroscience has established neurocognitive systems that act to maintain patterns of cognition in a particular task state (Cole et al., 2013; Duncan, 2010; Kam et al., 2018). However, experience such as mind-wandering

(Seli, Kane, et al., 2018; Smallwood & Schooler, 2006, 2015) suggest there are also intrinsic influences on these dynamics (Christoff et al., 2016; Smallwood, 2013a). One barrier to understanding self-generated influences on the dynamics of our thoughts is the lack of an empirical framework for understanding the mechanisms for transitions between neurocognitive states with different types of mental content. The current study examined whether naturally occurring changes in ongoing thought are rooted in macroscopic functional cortical organisation.

Contemporary cognitive neuroscience has established that neural functioning is organised along multiple hierarchies that together are assumed to give rise to the structure of human cognition (Mesulam, 1998). These hierarchies reflect different aspects of cognition including distinctions between unimodal and transmodal systems (Margulies et al., 2016), dissociations between sensory systems (C. Murphy, Rueschemeyer, Smallwood, & Jefferies, 2019), and neurocognitive patterns linked to complex task performance (Duncan, 2010; Shine et al., 2019). These hierarchies govern the topography of neural activity (Duncan, 2010; C. Murphy et al., 2018; C. Murphy, Rueschemeyer, et al., 2019; Sormaz et al., 2018) and our study tested whether this constraint extends to transitions between different cognitive states, and in particular the dynamics of off-task thinking. Off-task experiences are common in daily life, suggesting they are an important feature of human cognition (Killingsworth & Gilbert, 2010; Poerio et al., 2013), and prior laboratory studies have shown that they increase with the passage of time (Seli, Carriere, et al., 2018; Smallwood et al., 2002; Adam Turnbull et al., 2019).

In the current study we built on these findings to focus on the dynamics of off-task thought, which can be captured in a straight forward manner using multi-dimensional experience sampling (MDES). This method requires participants to provide intermittent descriptions of the contents of ongoing thought along multiple dimensions (Klinger & Cox, 1987). Recent work has used this method to reveal both the similarities and differences in the patterns that of ongoing thought take in the lab and in daily life (Nerissa Siu Ping Ho, Elizabeth, & Smallwood, 2020). Importantly in the context of this project, laboratory studies using MDES have captured a pattern off-task thought that increases with the passage of time (Poerio et al., 2013; Seli, Carriere, et al., 2018; Smallwood et al., 2002; Adam Turnbull et al., 2019), suggesting that this approach provides a viable subjective window into an important dynamic feature of human

cognition. Finally, prior studies that have combined experience sampling during tasks with measures of neural function have highlighted activity in multiple large scale systems during periods of off task thought. These networks include the default mode network (Allen et al., 2013; Christoff et al., 2009; Hasenkamp et al., 2012; Stawarczyk, Majerus, Maquet, et al., 2011) as well as regions linked to executive control (Christoff et al., 2009; A Turnbull et al., 2019).

In our study, participants performed a simple cognitive task while neural activity was measured using functional magnetic resonance imaging (fMRI). Multi-Dimensional Experience Sampling (MDES (Smallwood & Schooler, 2015)) was used to measure moment-to-moment fluctuations in individuals' experiences. We used these data to derive descriptions of the neural topography associated with the passage of time, and during off-task thought. We selected three well-established neuro-cognitive hierarchies reflecting (i) the distinction between unimodal and transmodal systems, (ii) visual and sensorimotor systems, and (iii) the patterns describing the brains response to cognitive tasks, identified in a previous study (Margulies et al., 2016). Using these spatial maps as descriptions of the constraints neural hierarchies place on function, we tested whether they provide a framework to understand the dynamic changes that characterise transitions between states of external task focus and off-task self-generated experiences. If neural hierarchies constrain the temporal dynamics linked to off-task thinking then (a) neural changes associated with the passage of time should match the topographical motifs seen in one or more neurocognitive hierarchies, (b) the same topographical neural motifs will be seen during patterns of off-task thought, and (c) the extent of these temporal changes should be related to individual variation in patterns of ongoing thought.

6.3 Results

6.3.1 Brain Regions Changing with the Passage of Time

We used a task in which people intermittently make behavioural responses to nominated target stimuli. It had two conditions, one requiring continuous monitoring (1-back) and another that did not (0-back, See top left hand panel of Figure 1 and Figure 5). In this context, we assume patterns of externally focused task-relevant cognition are momentarily established when participants make a response in the task. We used these moments as a reference point from which temporal changes can be

calculated, generating a regressor describing for each non-target the amount of time passed since the last behavioural response (range = 2.1-15.8s). Using this as an explanatory variable in a whole-brain analysis we found no regions that increased over time, however, multiple regions showed the reverse pattern (see Figure 1, and Supplementary Table 2). Regions that decreased activity over time included parts of visual and attention networks. Meta-analytic decoding (Yarkoni et al., 2011) confirmed these regions are involved in external task performance (see Figure 1).
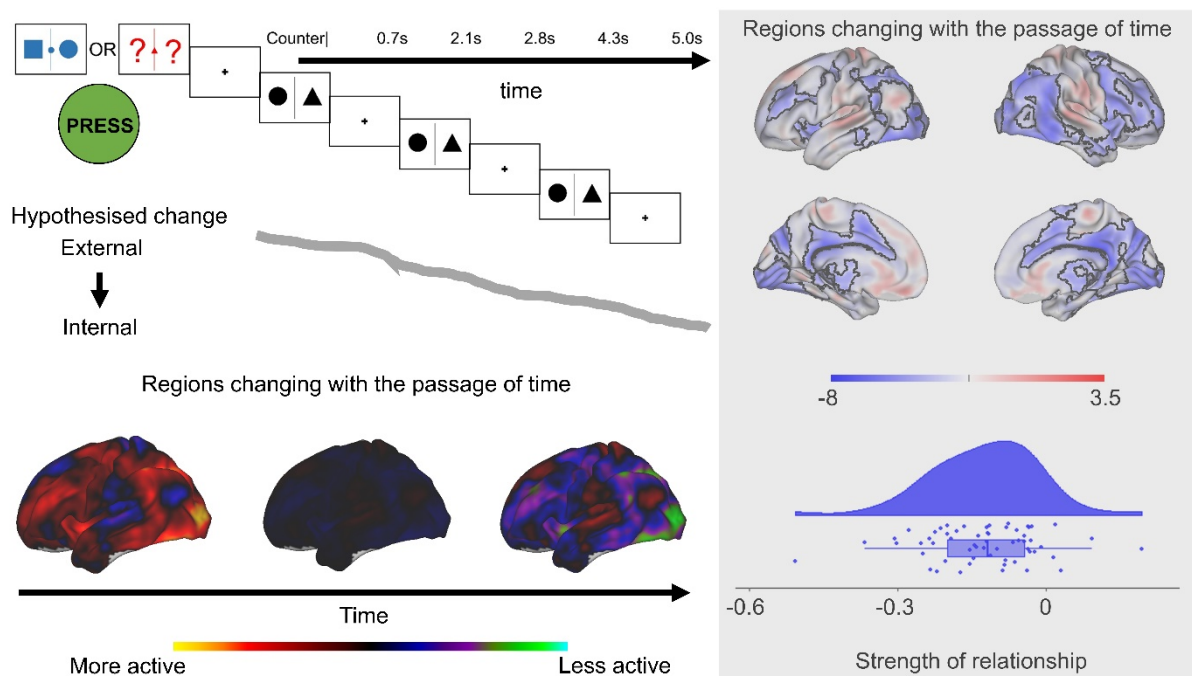
Figure 1. Brain regions change over time following task performance. This analysis looked for significant relationships between brain activity and the passage of time following a task event (target or thought probe: top right). This was based on the idea that external attention is established during external behaviour and then becomes subject to intrinsic influences with the passage of time while the participant remains uninterrupted. We found several large clusters of activity that showed a pattern of significantly decreasing activity with each non-target trial after the performance of an action (left). The global change in activity over time is represented by the unthresholded images in the bottom left. Neural results in the right hand panel are corrected at a cluster forming threshold of Z>3.1, FWE-corrected p<.05.

6.3.2 Gradient Similarity of Elapsed Time

Having documented how neural responses following task events change with time, we next examined whether the global topography of this pattern relates to either of the three neural hierarchies identified in our prior analyses (Margulies et al., 2016) (Figure 2). After extracting the similarity of each participants' elapsed time effects to each hierarchy (see Methods and Fig 2), a series of one-sample t-tests determined

neural patterns emerging with the passage of time show a significant association to (i) the modality gradient (t(58)=-8.457, p<.001) and (ii) the gradient highlighting the brain's response to a task (t(58)=-4.878, p<.001). There was no association with the transmodal gradient (t(58)=0.395, p=.694). In our task, therefore, the effect of time on neural activity can be effectively characterised as neural changes along two functional hierarchies - away from visual processing and regions implicated in task-positive processes.
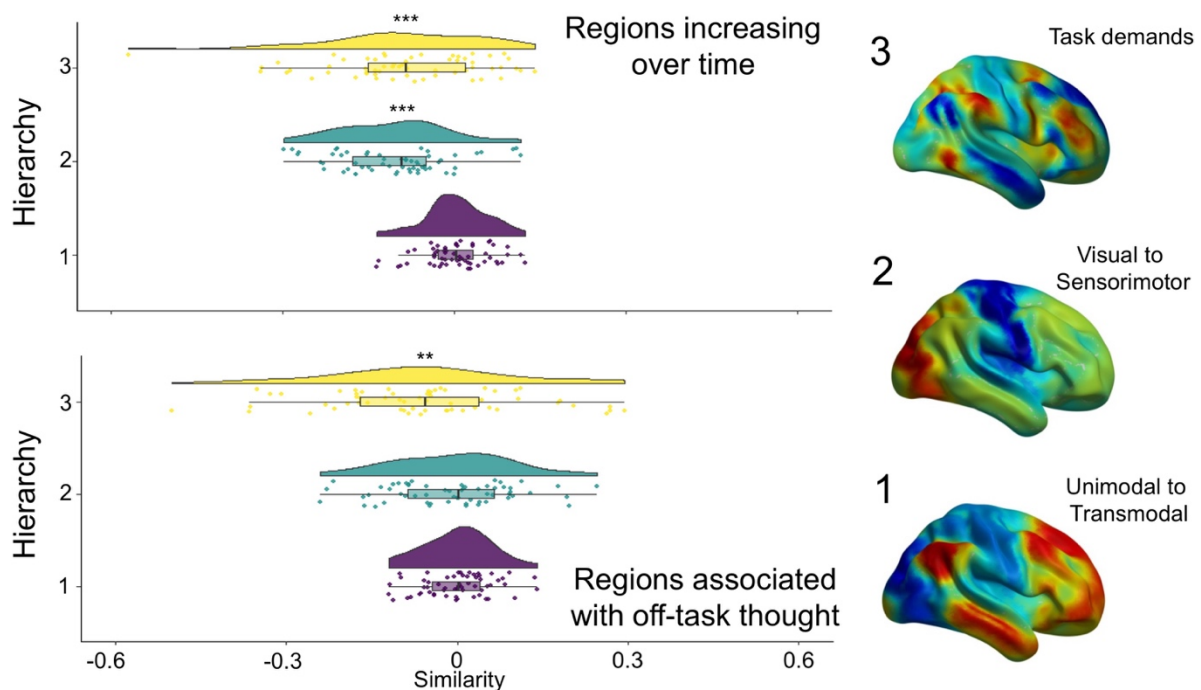
Figure 2. The brain dynamics associated with the passage of time can be understood as changes along neurocognitive functional hierarchies. The maps representing each participants' neural correlation with time were compared to previously defined functional hierarchies (Margulies et al., 2016). Brain regions that changed over time were significantly related to the hierarchies representing task-demands as well as modality (top). When participants said they were having off-task thoughts neural patterns were similar to patterns seen in the absence of external demands (bottom).

6.3.3 Relationship between Task-related Gradient Similarity and Off-task Thought

We next examined whether neural changes emerging over time are similar to the topographical patterns seen during off-task thought. We used spatial maps describing patterns of off-task thought derived from this data set and published in our prior paper (A Turnbull et al., 2019). A simple correlation between the off-task map and the elapsed time map found that these were similar (r = .46). Next, using a similar

approach as in our prior analyses (see Methods), we compared each participants' brain activity during off-task thought to each of the three neurocognitive hierarchies (Figure 2). This revealed the off-task spatial map shows a similar topography only to the task-related gradient (Gradient 3: $t(58)=-2.944$, $p=.006$; Gradient 1: $t(58)=0.100$, $p=.921$; Gradient 2: $t(58)=-0.678$, $p=.500$). To formally understand this similarity, we tested the distributions of off-task thought and regions that increased over time in terms of their similarity to the task-related gradient, and found no statistical evidence of a difference ($D=0.644$, $p=.801$, see Methods). This establishes that patterns observed with the passage of time, and during off-task states, have a similar neural topography that entails reductions in neural motifs that reflect the brains' response to tasks. All of these relationships are represented in the 3D scatter plot in the top right panel of Figure 3.
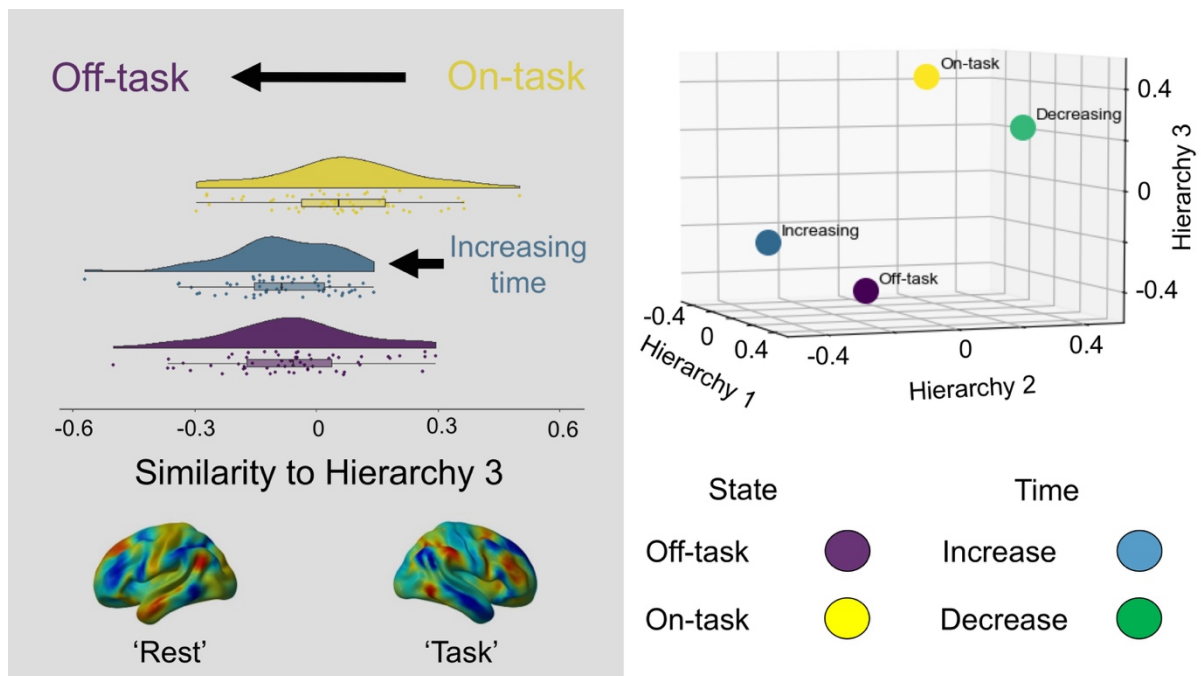
Figure 3. Neural dynamics associated with the passage of time and differences between on- and off-task thought are associated with common reductions in task positive regions. Brain activity during on-task thought looks similar to the task-positive end of the task-related gradient, as do regions that decrease over time. This suggests that over time a neural motif emerges that is similar to that seen during off-task thought, and mimics the patterns seen in the absence of a task (left). These same maps can be represented in a three-dimensional space based on each hierarchy (top right). In this plot it can be seen that neural patterns that decline over time (green), and patterns seen during on task states (yellow), are located in the top right quadrant. In contrast, patterns that increase over time (blue) and those associated with off task thought (purple) are located in the bottom right quadrant. Note that the values in the 3D plot are r-values from the group level results (including motion as a covariate) and are therefore related to, but not the same as, the beta-weights representing each subject's similarity score displayed in the raincloud plots (Allen, Poggiali, Whitaker, Marshall, & Kievit, 2018).

6.3.4 Individual Variation in Elapsed Time and Changes in Off-task Thought
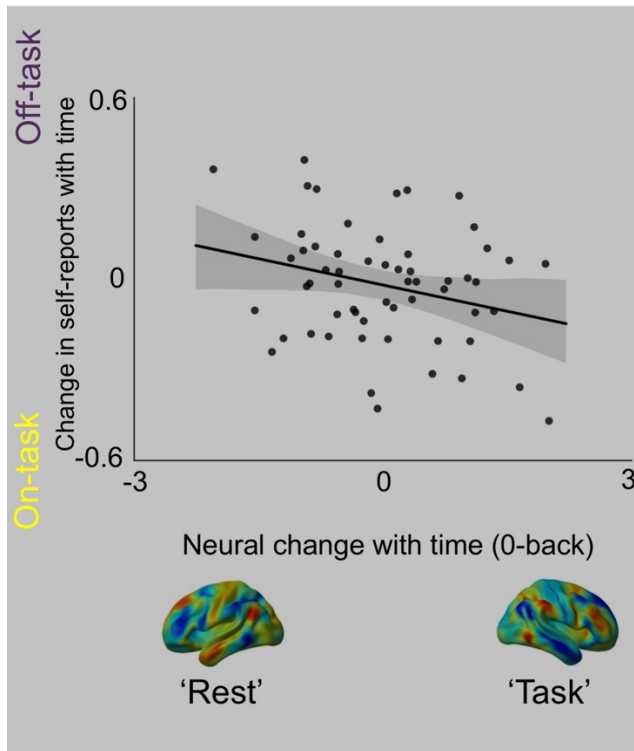
Figure 4. Greater neural shift towards task-negative regions during the 0-back task are associated with greater off-task thought. The horizontal axis of the scatter plot indicates the association between patterns of off-task thought and time. The vertical axis of the scatterplot indicates the change along the task positive hierarchy (Gradient 3) with the passage of time during the 0-back task. It can be seen that individuals who show the greatest shift away from task-positive regions during the 0 back task with time also show the strongest increase in off-task thought over time.

Finally, we examined whether neural changes that emerge over time have a direct association with the participants' self-reports of off-task thought. We extracted the weightings of the off-task thought component from each probe and calculated for each individual how this changed with time (see Methods). We ran a repeated measures ANOVA in which the change along each neural hierarchy with time in each task were the explanatory variables and the change in off-task thought with time in each task were the outcome variables. This revealed a main effect of the change along hierarchy 3 in the 0-back task $(F(1,49)=4.861, p=.032)$. Figure 4 plots the change in neural processing with time in the 0-back task against the average change in off-task thought over time. It can be seen in the scatter plot that those individuals who showed topographical changes in neural activity most strongly related to reductions in the patterns seen during active external task performance during the 0-back task, also showed the greatest overall shift to off-task thought with the passage of time. It is also clear that individuals who tended to maintain activity in task positive systems with time, tended to maintain better task focus. Together these analyses show that changes in the relative balance between task positive and task negative systems parrallel changes in participants self-reports of whether they were focused on the task or on other personally relevant information.

6.4 Discussion

Together our study establishes topographical changes in neural processing that emerge over time and those seen during off-task thought can both be understood as a common shift away from neural motifs seen during complex task performance (Duncan, 2010). Our study used an experimental procedure that allows the passage of time to be calculated from moments when external focus is established, and so provides novel support for studies that use complex statistics to highlight the association between hidden neural dynamics and self-generated cognitive states (Denkova, Nomi, Uddin, & Jha, 2019; Kajimura, Kochiyama, Nakai, Abe, & Nomura, 2016; Mooneyham et al., 2017; Vidaurre et al., 2017). It also complements work suggesting that the brain flexibly is temporarily reconfigured into states that support task performance (Shine et al., 2019) by providing an understanding of how these states are disengaged over time following a task event. Previous studies have shown that the brain takes minutes to return to a stable baseline following task performance (Barnes, Bullmore, & Suckling, 2009). Our study provides a snapshot into the subjective correlates of these temporal dynamics, helping align neural and psychological perspectives.

Although our study highlights links between neural changes over time and the emergence of self-generated states, many important questions remain unanswered. First, our study highlighted a general pattern of how neural activity changed with time across both the 0-back and the 1-back task. In a previous study using trait-level variation in neural architecture (Adam Turnbull et al., 2019) we identified networks related to increasing off-task thought over time across both tasks. However, studies using self-reports highlight temporal dynamics in experience are often contextually bound; for example in this paradigm stronger increases in off-task thought with time are seen in the easier 0-back task in longer sessions outside the scanner (Adam Turnbull et al., 2019). Similarly, the results of this study identified that the overall degree to which an individual switched towards an off-task state with the passage of time was associated with neural changes away from patterns associated with task states over time in the 0-back task. More generally, it is clear that not all individuals show the same degree of neural changes away from task relevant material with the

passage of time (see Figure 4). It remains unclear, therefore, the degree to which temporal changes in neural activity are bound to specific task conditions, or reflect features of an individual that influence whether, and to what degree, their attention is likely to switch away from the task in hand. Our correlational design cannot address this question, so future work using transcranial magnetic stimulation or lesion paradigms in neurological patients may be needed to understand if causally disruptions to regions such as dorsolateral prefrontal cortex (DLPFC) or thalamus influence how neural processing changes with time. Additionally, it is also possible that increasing the difficulty gradient between the task conditions (e.g. by increasing memory load) would enable us to see differences in neural dynamics across the two tasks in the population as a whole.

Second, the observed topographical changes in neural function with time must be partly determined by the specific capacities that our tasks involve (e.g. attention, visual processing, and working memory). Accordingly, it is important to explore how time influences neural activity in contexts with richer semantic and sensory features (such as reading, listening to audiobooks, or watching movies). In these conditions prior work has highlighted regions within the default mode network as important in maintaining task focus (Zhang, Savill, Margulies, Smallwood, & Jefferies, 2019). It is possible that under these conditions regions of the default mode network may play a role in scaffolding attention over time because of their association with regions linked to semantic (Ralph, Jefferies, Patterson, & Rogers, 2017) or episodic memory (Moscovitch, Cabeza, Winocur, & Nadel, 2016).

Third, it is important to bear in mind that while our study highlights associations between patterns of off-task thought over time with neural dynamics that emerge over time, this association could emerge for many reasons. For example, motivation is known to play an important role in maintaining on task attention (Seli, Carriere, et al., 2015), suggesting that part of the observed change in neural function may reflect relatively deliberate shift in the focus of ongoing thought. Finally, while our analysis highlights how changes in neural function are linked to patterns of off task thought, this type of observation does not substantially constrain accounts of why time should lead to alternative patterns of thought (Smallwood, 2013a). In our prior study examining momentary differences in neural activity (A Turnbull et al., 2019), we found that a set of neural processes rooted in DLPFC, govern the regulation of off-task thought with

respect to the current level of tasks demands. It is possible, that changes in neural activity over time reflects the hypothesised modulatory influence of the ventral attention, or salience, network on patterns of cognition (Badre & Nee, 2017; Dosenbach et al., 2008; Dosenbach et al., 2007; Sridharan et al., 2008). Alternatively, brain systems focused on the thalamus may play an important role in orchestrating how neural processes change over time, given their documented role in organising task relevant neural processing (Shine et al., 2019). Alternatively, it is possible that a pattern of task adaption in task positive regions that emerge with the passage of time could allow neural activity to shift away from the task relevant state. Thus, although our study establishes that temporal neural changes are at the core of how patterns of ongoing thoughts emerge over time, it leaves open the neural mechanism through which changes over time allows our minds the freedom to consider events other than those in our immediate environment.

6.5 Methods

6.5.1 Participants

A group of 63 young adults took part in a task-based fMRI study during which we used MDES during task performance to gain descriptions of experience at specific moments in time. After excluding participants (see Method Details) 59 participants (36 females, mean age=20.17 years, S.D.=2.24 years) remained for data analysis. These data have been analysed before to understand the neural basis of off-task thought (A Turnbull et al., 2019). A subgroup of 34 participants were scanned twice for the data used in Sormaz et al. (Sormaz et al., 2018). All participants were native English speakers, with normal/corrected vision, and no history of psychiatric or neurological illness. All participants were acquired from the undergraduate and postgraduate student body at the University of York. Both experiments were approved by the local ethics committee at both the York Neuroimaging Centre and the University of York's Psychology Department. All volunteers gave informed written consent and were compensated in either cash or course credit for their participation. This experiment was carried out in accordance with the relevant guidelines and regulations.

6.5.2 Task Performance

Task performance was identical to that used in the prior studies using this data (Sormaz et al., 2018; A Turnbull et al., 2019), and is similar to a task used in previous

studies (Poerio et al., 2017; A Turnbull et al., 2019; Vatansever et al., 2018). Experience was sampled in a task paradigm that alternated between blocks of 0-back and 1-back to manipulate attentional demands and working memory load (see Figure 5). Non-target trials in both conditions were identical, consisting of black shapes (circles, squares, or triangles) separated by a line. In these trials the participant was not required to make a behavioural response. The shapes on either side of the line were always different. The colour of the centre line indicated to the participant the condition (0-back: blue, 1-back: red; mean presentation duration=1050ms, 200ms jitter). The condition at the beginning of each session was counterbalanced across participants.

During target trials, participants were required to make a behavioural response on the location of a specific shape. On these trials in the 0-back condition, a pair of shapes were presented (as in the non-target trials), but these were blue. Participants were instructed to indicate which shape (left or right) matched a small blue shape in the centre of the line down the middle of the screen. In the 1-back condition, the target trial consisted of two red question marks either side of the central line (in place of the shapes). There was a small shape in the centre of the screen as in the 0-back condition, but it was red. Participants had to indicate via button press which of the two shapes from the previous trial matched the central shape. Due to an error during data collection, reaction time was not measured during this task and accuracy was measured by the last button press during target trial presentation.

The contents of ongoing thought during this paradigm were measured using multi-dimensional experience sampling (MDES) (Smallwood & Schooler, 2015). MDES probes occurred instead of a target trial on a quasi-random basis. When a probe occurred the participants were asked how much their thoughts were focused on the task, followed by 12 randomly shuffled questions about their thoughts (see Supplementary Table 1). All questions were rated on a scale of 1 to 4.

Each run was 9-minutes in length and there were four runs per scanning session. In each run, there was an average of six thought probes (three in each condition), so that there were on average 24 (SD=3.30, mean=12 in each condition) MDES probes in each session.
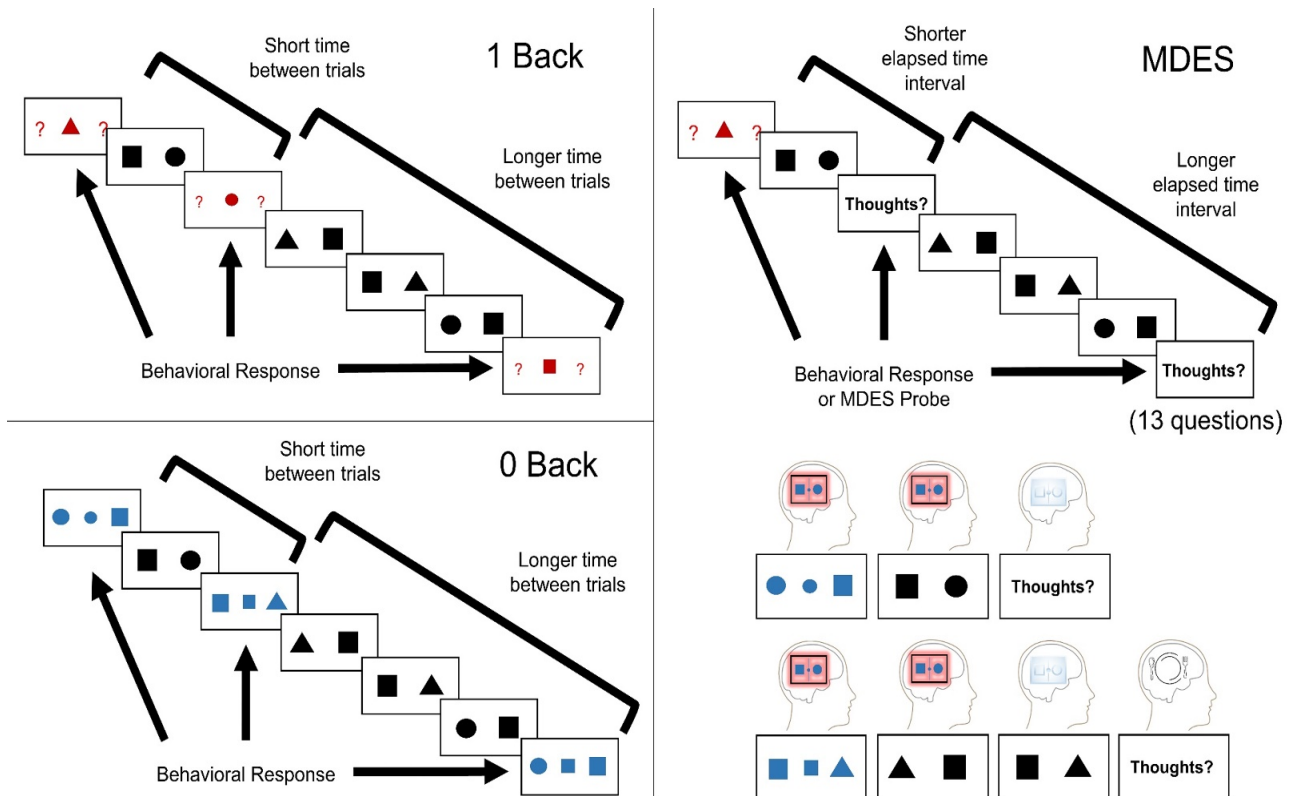
Figure 5. The task consisted of two conditions. In both conditions, participants had to make a spatial decision on the location of a shape shown in the middle of the target trial. In the 0-back, they had to say which side of the screen the shape was on during that trial (perceptually-guided decision). In the 1-back, they had to say which side of the screen the shape had been on the previous trial (memory-guided decision). On a quasi-random basis, the target trials were replaced by thought probes that asked 13 questions about the participants' thoughts. These always started with a question about task focus, then the other 12 question (see Supplementary Table 2) were in a random order.

6.5.3 fMRI Acquisition

fMRI acquisition follows a standard protocol used in studies in this laboratory, including those using the same data as this study (Sormaz et al., 2018; A Turnbull et al., 2019) and others (Adam Turnbull et al., 2019). MRI scanning was carried out at the York Neuroimaging Centre. Structural and functional data were acquired using a 3T GE HDx Excite MRI scanner with an eight-channel phased array head coil tuned to 127.4 MHz. Structural MRI acquisition was based on a T1-weighted 3D fast spoiled gradient echo sequence (TR=7.8s, TE=minimum full, flip angle=20º, matrix size=256x256, 176 slices, voxel size =1.13x1.13x1mm). Functional data were recorded using single-shot 2D gradient echo planar imaging (TR=3s, TE=minimum full, flip angle=90º, matrix size=64x64, 60 slices, voxel size=3mm isotropic, 180

volumes). A FLAIR scan with the same orientation as the functional scans was collected to improve coregistration between scans.

6.5.4 Data Pre-processing: fMRI

Data pre-processing was carried out in a similar way to previous studies using this data (Sormaz et al., 2018; A Turnbull et al., 2019). Two participants were excluded for falling asleep. Task-based 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). The functional data were pre-processed and analysed using the FMRI Expert Analysis Tool (FEAT). The individual subject analysis first involved motion correction using MCFLIRT and slice-timing correction using Fourier space time-series phase-shifting. After coregistration to the structural images, individual functional images were linearly registered to the MNI-152 template using FMRIB's Linear Image Registration Tool (FLIRT). Functional images were spatial smoothed using a Gaussian kernel of FWHM 6mm, followed by grand-mean intensity normalization of the entire 4D dataset by a single multiplicative factor, and highpass filtered (Gaussian-weighted least-squares straight line fitting, with sigma=100s). Following pre-processing, the amount of participant head motion in each scan was inspected. Scans in which there was more than 1mm absolute head motion or more than 0.2mm relative head motion were discarded. Two participants were excluded due to having more than two runs removed. In total, three participants had one out of four runs removed due to motion and three participants had two out of four runs removed. Due to the possibility that motion could change over time following the motor action during external task performance, more stringent motion correction procedures were used than in previous studies using this data (Sormaz et al., 2018; A Turnbull et al., 2019).

6.5.5 Principal Component Analysis

Behavioural analyses were carried out in SPSS (Version 24.0, 2016). The scores from 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 (Poerio et al., 2017; Sormaz et al., 2018; A Turnbull et al., 2019; Adam Turnbull et al., 2019; Vatansever et al., 2018) we concatenated the responses

of each participant in each task into a single matrix and employed a PCA with varimax rotation. PCA was used in previous studies to establish the structure of ongoing thought across different conditions, and the same analysis has been used here to allow comparison with measures of off-task thought in those studies. We performed the same analysis with a rotation that does not induce orthogonality (oblimin), and found that none of the factors correlated above 0.25 suggesting that varimax rotation was appropriate (Tabachnick, Fidell, & Ullman, 2007). Four components were selected based on the inflection point in the scree plot (see Figure 6). These were defined (in order of decreasing eigenvalue) as Task-relatedness, Detail, Modality, and Emotion of thought based on their question loadings (Table 1). For the purposes of this study, only the task-related component was used for analysis. The loadings of each questions on this component can be seen in Figure 7 in the form of a wordcloud.

	Component			
	1	2	3	4
Deliberate	.739	.258	-.134	-.002
Detailed	.350	.569	-.044	.214
Emotion	.381	-.090	.249	.675
Evolving	.145	.533	-.217	.267
Focus	.770	.096	.008	-.033
Future	-.219	.334	.017	.511
Habit	-.023	.612	-.025	.060
Images	.001	.183	.781	.150
Other	-.577	.043	.192	.449
Past	-.158	.157	-.146	.538
Self	-.571	.369	.017	.034
Vivid	-.080	.719	.244	-.013
Words	.160	.152	-.785	.124

Table 1. Factor loadings for the 13 questions used to assess ongoing thought on the 4 PCA factors. Only factor 1 was used in this study.
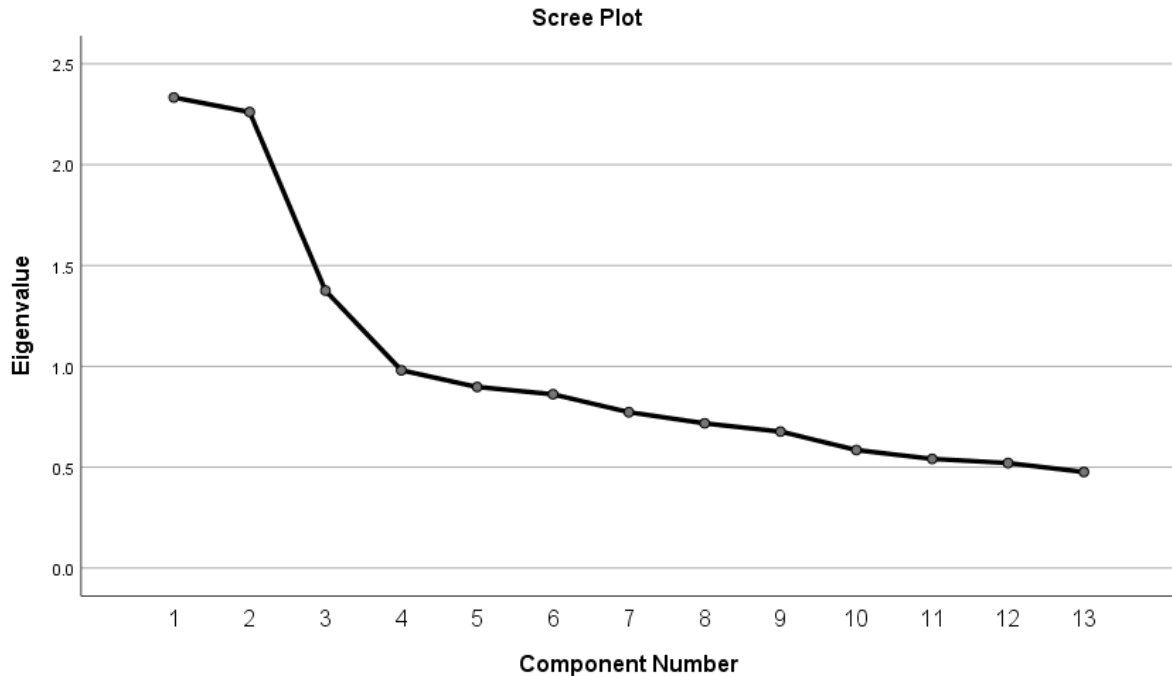
Figure 6. Four components were chosen from the screen plot following a PCA on the answers to 13 thought-related questions. For this study, only the first component (task-related thought) was used for analysis.

6.5.6 Task-based fMRI Analysis

Task-based analyses were carried out in FSL (FSL version 4.1, http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FEAT). The design files for this analysis can be found along with the rest of the details of the analyses in this paper at: https://github.com/adamgeorgeturnbull/elapsed_time. All explanatory variables (EVs) were convolved using FSL's gamma function. EVs were modelled for the full duration of both non-target trials and correct target trials (incorrect trials were not included) in each condition separately. Any runs in which participants only made one correct response or fewer in either task were excluded. In total, four participants had one out of four runs removed, and one participant had two out of four runs removed. None of the participants who had runs excluded for poor task performance also had runs removed for motion. In addition to modelling the non-target and target trials, moderator EVs were included that modelled the length of the mini-block (since the last time the participant had to make a judgement during either a target trial or MDES probe). This was calculated by starting a counter at the end of the first non-target trial following a target event and adding the time for each non-target until either a target or MDES

probe, in which case the counter was re-started. One moderator EV was added for time for the non-targets in each condition, and one for the targets. These EVs were mean-centred within each run. This gave a total of 8 EVs: four simple boxcar functions (two per condition for both non-targets and correct targets) and four moderators for these same time periods with mean-centred time since last event (see the right side of Figure 1). A range of contrasts were included for a full description of the results. The contrasts of interest were a positive correlation with time across both tasks, a negative correlation with time across both tasks, and contrasts between the two tasks (regions significantly more related to time in one condition than the other) for targets and non-targets. The significant clusters can be seen in Supplementary Table 2. Fixed level analyses were performed for each participants included runs to provide an average brain response per person. Group level analyses were carried out using a cluster-forming threshold of $Z>3.1$ and a whole-brain correction at $p<.05$ FWE-corrected (Eklund et al., 2016). Average framewise displacement was included at the group level to additionally control for effects relating to this nuisance variable. Figures were made using Connectome Workbench.

6.5.7 Gradient Similarity Analysis

To assess to what extent the results of this fMRI experiment were occurring in the gradient space defined by Margulies et al. (Margulies et al., 2016), we performed a gradient similarity comparison. For each participant's run-averaged brain response (fixed level output whole-brain zstat map) for significant contrasts of interest, we performed a spatial correlation using fsl_glm (demeaned using --demean) within a cortical mask defined by the regions included in the gradient. This gave three beta weights for each person representing how similar their brain response for each contrast was to each of the first three gradients defined by Margulies et al. (Margulies et al., 2016). To understand how the brain's dynamics during task performance related to on- and off-task thought, this analysis was also carried out on the individual subject average brain responses for on- and off-task thought calculated in Turnbull et al. (A Turnbull et al., 2019). One-sample t-tests were carried out on these beta-weights to assess whether the group similarity of these responses was significantly related to any of the three gradients. These were Bonferroni corrected for multiple comparisons (alpha=.008). To directly compare the distributions of off-task thought and dynamic changes in terms of their relationship to the task-related gradient, we performed a

Kolmogorov–Smirnov test in SPSS (see Results). Figures were made in R using raincloud plots (Allen et al., 2018).

6.5.8 Relationship to Changes in Off-task Thought

To examine whether there was a relationship between the changes in the brain over time during task performance in gradient space and the change in off-task thought, we extracted the counter score (representing the length of time since the last response event) for each MDES probe. The time since the last target or preceding thought probe was correlated with off-task thought within each participant in each condition. These values were Fisher z-transformed. There was negligible average change in thoughts over time (mean=0.0194, S.D.=0.19, t(58)=0.765, p=.447). Studies with longer time periods suggest that off-task thoughts increase over time in a way that relates to individual differences in cognitive performance (Smallwood et al., 2002; Adam Turnbull et al., 2019). The time periods here may be too short to identify these changes on a group level, however, the relationships that have been found to changes in neural function suggest they are sufficient to identify meaningful individual differences. We ran a repeated measures ANOVA in which the change along each neural hierarchy with time in each task were the dependent variables. The similarity of the neural elapsed time effects for non-targets to each of the three first gradients from Magulies et al. (Margulies et al., 2016) in each task were entered as covariates of interest. Framewise displacement, age, and gender were entered as covariates of no interest. Data were mean-centered before performing this analysis.

Chapter 7 – General Discussion

7.1 Introduction

The results from this thesis are important in two ways:

- By measuring ongoing thought using the same paradigm across two experimental conditions (over 3 days in the behavioural laboratory and during a single fMRI scanning session) with both trait and state fMRI they provide insight into the structure of ongoing thought with increased confidence in the use of this technique as a means of understanding the processes engaged during different states.

- By leveraging the specific design features of this paradigm they enable the delineation of the systems involved in different aspects of ongoing thought more clearly, helping to resolve debates in the literature. Using fMRI with MDES in two conditions allows systems involved in state maintenance in general to be separated from those involved in specific state maintenance, and including elapsed time enables the systems involved in state maintenance to be separated from those involved in state transitions (Smallwood, 2013a). These features are particularly useful in providing clarity in debates of whether executive control is involved in maintaining internal states (McVay & Kane, 2010; Smallwood, 2010; Smallwood & Schooler, 2006) and whether the DMN is unique to internal/task-negative states (Andrews-Hanna et al., 2014; Christoff et al., 2009; Crittenden et al., 2015; Konishi et al., 2015; Margulies et al., 2016; Raichle et al., 2001; R Nathan Spreng, 2012; R Nathan Spreng & Grady, 2010).

This general discussion will begin by summarising the results of this thesis on these two levels: those that provide validation of experience sampling and fMRI as a means of understanding the neurocognitive basis of ongoing thought, and those that further our understanding of the specific systems involved in different states. Following this, the results regarding the role of specific systems during ongoing thought will be embedded within a state framework. Particular attention will be paid to the role of executive control, which this thesis suggests is positively involved in both maintaining and transitioning to internal states. A specific section will be designated to

summarising the role of the DMN in ongoing thought to demonstrate how its link to determining state contents in this thesis points to a general role in using connections to memory and perception to guide behaviour in concert with the rest of the central nervous system. Finally, limitations to the generalisability of this thesis will be addressed, with suggestions for how future research can help to understand how the features of this paradigm uniquely bias the findings towards specific modalities and timescales.

7.2 Summary of Empirical Findings

7.2.1 Validation of Experience Sampling and fMRI

By using PCA to decompose the answers to 13 experience sampling questions, this thesis has shown that dimensions of thought can be reliably identified across different experimental conditions. These dimensions described thought along four dimensions: on- to off-task, vague to detailed, images to words (modality), and positive to negative emotional valence. The component describing levels of detail had positive loadings on the questions about detail, as well as specificity, vividness, and their evolving nature. The off-task component was negatively loaded on the questions about task focus and the deliberate nature of thoughts, and positively loaded on questions about whether thoughts were about the past, future, other people, and the self. The modality component separated thoughts in words from thoughts in images, and hence described the modality of thoughts along a dimension between these two extremes. Finally, the question asking participants about the emotional valence of their thoughts (positive or negative) was mostly isolated from all other questions to form a component of its own that varied between negative and positive emotional states. These components were identified using data collected over 25-minute sessions of task performance across three days as well as during a shortened version of this task in the fMRI scanner. Three out of four dimensions correlated highly in terms of their question loadings and levels within participants (emotional valence did not correlate significantly) across versions. This paradigm also successfully resulted in context-dependent regulation of experience across the two task conditions, with greater levels of on-task thought, detail, and thoughts in words in the 1-back across both versions.

The identification of these components reproduces results using similar analyses in this same cohort (Martinon, Riby, et al., 2019; Poerio et al., 2017; Sormaz

et al., 2018; Vatansever et al., 2018), and other cohorts (Konishi et al., 2017; Ruby, Smallwood, Engen, et al., 2013; Smallwood et al., 2016). Studies using similar approaches using dimensionality reduction of experience sampling data have identified related, but subtly different, dimensions of thought. A study using exploratory factor analysis on a larger group of questions asked retrospectively at the end of a single resting period found components describing the temporal nature of thoughts, as well as the emotional valence (Gorgolewski et al., 2014). Thoughts about other people largely formed their own component of thought. A second study using CCA to find shared components in this same questionnaire and brain connectivity found components describing deliberate thought, emotional thought, personally relevant thought, and one separating thought based on modality (H.-T. Wang, D. Bzdok, et al., 2018). Another study using hierarchical clustering found dimensions related to personal significance, temporal and emotional components, and level of abstraction or specificity (Andrews-Hanna et al., 2013). These studies show that there is a strong overlap in the structure of thought identified using experience sampling with dimensionality reduction, with some variation in the precise make-up of components that likely relates to the specific questions and experience sampling paradigms (see Limitations). Importantly, a recent study using experience sampling found similar components to those in this thesis in daily life, and these were found to be related to overlapping measures of brain structure and function to components identified in the lab (Ho et al., 2020). Together, these results highlight the fact that ongoing thought is multi-dimensional in nature, and suggest that dimensionality reduction approaches are a useful means of understanding its structure.

The data-driven dimensions of thought identified in this thesis were reliably linked to brain networks using fMRI, whether the analyses involved the trait architecture of the brain or in-the-moment state neural activity. The attention networks were consistently identified as correlating with task-related thought. Specifically, the connectivity of the dorsal attention network (DAN) was identified in a main effect relating to task-related thought across both tasks, and in a similar contrast looking at brain activity, a region in the DAN was identified by its relationship to in-the-moment on-task thought. The ventral attention network (VAN) was similarly related to task-related thought, but was significant in a contrast that included variations across task context both in terms of connectivity and activity. This contrast identified significant

associations with on-task thought in the 1-back and opposite associations (with off-task thought) in the 0-back. The default mode network (DMN) was not significantly related to off-task thought in any of these analyses, but instead was linked to the levels of detail in thoughts in analyses looking at both trait architecture and state activity, reproducing previous studies (Sormaz et al., 2018; Vatansever et al., 2018). These consistent results provide confidence in using experience sampling with PCA and fMRI as a means of understanding cognition, suggesting meaningful results can be obtained by combining these approaches (Martinon, Smallwood, et al., 2019). They also further demonstrate the trait-like nature of ongoing thought, showing that specific aspects of thought are related to measures of trait processing that are represented in resting state functional connectivity (Golchert et al., 2017; Gorgolewski et al., 2014; Karapanagiotidis, Jefferies, et al., 2019; Medea et al., 2016; Poerio et al., 2017; Smallwood et al., 2016; Vatansever et al., 2018; Villena-Gonzalez et al., 2018; H.-T. Wang, D. Bzdok, et al., 2018; H.-T. Wang, G. Poerio, et al., 2018; Zhang et al., 2019), and that these same processes are engaged in-the-moment during ongoing thought (Seli et al., 2016a) in a way that can be measured by task-based fMRI.

7.2.2 Specific Systems Engaged during Ongoing Thought

This thesis identified several dissociable neurocognitive systems that are engaged during ongoing thought:

- The VAN was involved in the context-dependent regulation of off-task thought: connectivity between the motor cortex and VAN, and activity in the DLPFC (in the VAN), both showed a pattern that related to off-task thought in the 0-back and on-task thought in the 1-back.
- The DAN was involved in transitioning between external and internal states, and activity in this network was increased during on-task states irrespective of task condition. Additionally, the functional and structural representation of signals from this network was important for allowing off-task thought to emerge, consistent with a role in external task states.
- As well as being related to the level of detail in thought, the DMN was consistently involved in determining state contents through its interaction with regions involved in external processing. The connectivity between this network and the visual cortex was related to the maintenance of task-related detail even

when it was not needed for task performance and segregating this network from signals from the DAN was important for allowing cognition to emerge that was unrelated to the task in the easier 0-back. This suggests an important role in the coupling and decoupling of cognition to external input that is important for maintaining states and determining their contents.

- The motor cortex was consistently related to task performance: the connectivity of this network to the VAN was positively related to task performance and the connectivity of this network to the lingual gyrus was related to performance-related states, suggesting a role in maintaining external task-specific states.

- Executive control was positively related to internal states in several analyses. DAN connectivity linked with transitions to internal states was positively related to fluid intelligence and creativity, and the DLPFC region involved in both internal and external states was shown to be related to executive processes by a meta-analytic decoding. Additionally, fluid intelligence was significantly related to transitions over time to internal states specifically in the less demanding 0-back task.

Together, these results show that the inclusion of multiple task conditions and elapsed time during MDES with associated fMRI provides a detailed picture of the dissociable roles different neurocognitive systems play in ongoing thought.

7.3 States of Mind: Theoretical Implications

Each moment in time can be thought of as a neurocognitive state that has a specific make-up in terms of component processes and contents. Using fMRI and experience sampling we can gain snapshots of these states from subjective report and BOLD activity patterns at any particular moment. At any point in time the brain can be considered either as existing in a period of state maintenance (held in a similar location of state space) or in a transition between states (moving along one or more dimension in state space). The experimental design of this thesis used this framework to better understand ongoing thought in two ways:

- Having two conditions that differ in their external demands encourages participants to maintain states differentially across the two conditions, as shown by the significant differences in off-task, detailed, and the modality of thoughts across the two tasks. Additionally, the use of these conditions allows processes

involved in maintaining specific states (e.g. external, on-task ones) to be separated from those involved in maintaining states more generally in line with external demands (e.g. external task states during difficult tasks and internal states during easier tasks). This section will first elaborate the findings related to state maintenance, beginning with those that are specific to internal and external states. It will then examine systems that are involved more generally in maintaining states in line with external demands, showing how this design helped to identify shared executive processes involved in both on- and off-task states.

- Including relatively infrequent external moments of task performance with large amounts of non-targets that require no action encouraged state transitions. Separating the processes involved in maintaining and transitioning between states in this way also enabled a better understanding of ongoing thought, by dissociating systems involved in transitions from those involved in maintenance (Smallwood, 2013a). This section will go on to outline the results related to state transitions, showing how transitions to internal states can relate positively to executive control and involve whole-brain reorganisations.

This section will end with a discussion of a specific finding that suggests the role of executive control in ongoing thought can only be understood by taking into account both transitions and external context.

7.3.1 Maintaining States

Much early research on mind wandering was focused on understanding it in the context of executive failure (Engle & Kane, 2004; Kane et al., 2007; McVay & Kane, 2009, 2010, 2012a, 2012b; McVay et al., 2009). Thinking in terms of states, doing an attention task like those predominantly used to study 'mind wandering' (I. H. Robertson et al., 1997) requires the maintenance of a visual, externally focused state. In this context, a failure to maintain that state leading to a transition to an internally focused state will lead to an error (O'Connell et al., 2009). This simple example highlights three key aspects of state maintenance. The first is that internal states are characterised by an attenuation of external input, a process known as perceptual decoupling (Kam & Handy, 2013). The second is that external states relate to task performance and need to be maintained during tasks. The third is that the current state needs to be adjusted

to match the demands of the current situation. Maintaining an internal state in a circumstance where there are low external demands can be a more fruitful use of that time, as internal states can involve contents that are beneficial to mood (M. S. Franklin, Mrazek, et al., 2013; McMillan et al., 2013), useful in planning the future (Baird et al., 2011; Gerlach et al., 2011; Gerlach, Spreng, Madore, & Schacter, 2014; Jing et al., 2016; Stawarczyk et al., 2013; Thakral et al., 2017) and creative problem solving (Baird et al., 2012; Smeekens & Kane, 2016; Yamaoka & Yukawa, 2019; Zedelius & Schooler, 2015). This need to match current state to the demands of the external environment is known as context regulation (Andrews-Hanna et al., 2014). This thesis provides several findings that help us better understand these aspects of state maintenance:

- The interaction of the DMN and regions involved in external processing is important for perceptual decoupling.
- The motor cortex plays a role in external state maintenance through an involvement in task performance.
- Executive processes within the VAN are involved in flexibly adjusting state maintenance so that it is appropriate for the demands of the current situation.

7.3.1.1 Maintaining Internal States: Perceptual Decoupling

The limits to the global workspace of consciousness necessitates competition for resources between internal and external states (Kam & Handy, 2013; Smallwood, 2010). This is an extension of theories of perception that show that each visual object initially competes for resources but, once selected, it is prioritised by the interaction of multiple brain systems (Duncan, Humphreys, & Ward, 1997). As a visual object, once selected, takes resources from other parts of the visual field, a transition to an internal state results in the attenuation of external input more generally (Kam & Handy, 2013). This process, known as perceptual decoupling, has been shown to occur in a range of studies (Barron et al., 2011; Kam et al., 2013; Kam & Handy, 2013; Kam et al., 2014; Kang et al., 2014; Konishi et al., 2017; Smallwood et al., 2011). Studies using fMRI have shown the DMN to be involved in a range of perceptually-decoupled processes (Konishi et al., 2015; C. Murphy et al., 2018; C. Murphy, Wang, et al., 2019; Smallwood, Tipper, et al., 2013), and internal states can be causally linked to increased connectivity within the DMN (Kajimura et al., 2016).

Results from this thesis suggest that the functional architecture of the DMN at rest is important for perceptual decoupling. In a seed-based analysis, functional connectivity between the DMN and visual regions was found to relate to levels of task-related detail in participants' thoughts in a way that varied over time and across conditions. Separating participants by their connectivity showed most clearly that participants with high connectivity had consistently high levels of detail across both tasks, whereas participants that decoupled these regions had detail that dissipated during the 0-back. Similarly, a network analysis found that segregating regions in the DAN that were active during on-task thought from the DMN specifically within the DLPFC at rest was related to allowing more time to be spent in internal states during the easier 0-back task. These results suggest that the DMN plays a role in determining state contents through interactions with regions that are involved in external processing. This role is in line with conceptualisations of the DMN as a hub of brain function (Rogers et al., 2004), integrating multimodal information (Margulies et al., 2016; Mesulam, 1998). These results also add to research showing that segregating external signals from the DMN at rest is important for allowing perceptually decoupled processing (Hong et al., 2019; Margulies et al., 2016; C. Murphy, Wang, et al., 2019). Additionally, in an analysis looking at relationships between brain architecture and autistic traits, connectivity between the lingual gyrus (in the visual cortex) and regions involved in theory-of-mind was related to deficits in imagination. This result suggests that the functional segregation of visual regions from higher order regions in order to decouple processing from perception (Margulies et al., 2016; C. Murphy, Wang, et al., 2019) extends to real-world measures of cognition, and may be altered in autism, in line with research showing decreased functional segregation in autistic participants at rest (Hong et al., 2019).

The repeated identification of visual regions relating to ongoing thought also highlights the importance of the coupling and decoupling of attention to external signals when determining state contents. It is also is in line with research that shows that these regions contain information about the contents of both internal and external states (Horikawa & Kamitani, 2017; Horikawa et al., 2013; Kamitani & Tong, 2005; Miyawaki et al., 2008; Reddy et al., 2010). It is not yet known exactly how these regions interact with the rest of the brain in order to provide perceptual details to thought that is unrelated to incoming visual information, and how this differs from coupling to vision.

For example, in this thesis it appears that coupling the DMN to vision at rest is related to providing task-related details to thoughts, but this type of coupling has also been linked to providing internal states with contents (Villena-Gonzalez et al., 2018). It is theorised that these differences may emerge from the direction of information flow, which cannot be determined using functional connectivity at rest (Ishai, Ungerleider, & Haxby, 2000). This is supported by an EEG study suggesting that "top-down" signals are involved in the production of visual imagery, whereas "bottom-up" signals dominate during perception (Dentico et al., 2014). Research applying directional modelling approaches to fMRI data found that frontal-visual coupling was modulated by an interplay between "top-down" and "bottom-up" signals during perception, while only "top-down" signals were involved during imagery (Dijkstra et al., 2017). It may be that the functional segregation of the DMN from visual regions at rest represents a more flexible trait ability to engage these processes in real time to allow perceptual decoupling, supported by the fact that participants with increased connectivity only showed differences in the levels of task-related detail in the easier 0-back.

In-the-moment fMRI data gives more insight into how processing in task-related regions is engaged in real time, providing additional insight into the process of perceptual decoupling. By modelling each non-target trial and including time as a covariate, an analysis in this thesis found that a large number of regions across the brain were less active during each subsequent non-target without interruption. These included visual and attentional regions, suggesting an attenuation of processing in these regions over time following task performance. This result suggests that perceptual decoupling involves multiple large-scale networks that may act to support the internal focus of attention once it has gained access to the global workspace (Kam & Handy, 2013). This result also suggests that this is a gradual process that seems to deepen as the internal state is maintained for longer. A study using a similar analysis to identify low dimensional changes in brain activity during task performance found that the pattern explaining the highest variance also loaded highly on visual regions (Shine et al., 2019): they found that the brain moved towards a visual pattern of activity during task performance. These changes may represent the other side of the perceptual decoupling coin, with vision being coupled to external attention specifically during task performance and then attenuating over time as the participant moves back into an internal state. Further research is needed to understand the extent to which

these changes in activity patterns coincide with altered information flow in the brain, and how this allows perceptually decoupled processing to emerge.

7.3.1.2 Maintaining External States: the Motor Cortex

In this thesis, the motor network showed multiple links to states that were important for task performance. Firstly, in a seed-based functional connectivity analysis the motor cortex was identified as significantly more correlated with the VAN in participants who showed greater context regulation of off-task thought. This means that participants who altered the states they maintained in line with task context showed greater connectivity between these two networks. This connectivity was also related to overall improved task performance, suggesting a role in task-related state maintenance. Over and above activity during performance itself, neural processing in the motor cortex has been shown to be important for the preparation and adaptation of upcoming task performance: recent studies have shown a close link between trial-by-trial preparatory signals in the motor cortex and effective modulation of processing in real time to reduce errors (Vyas, O'Shea, Ryu, & Shenoy, 2020). Internal states are known to interfere with these processes (Kam et al., 2012; Kam & Handy, 2013) highlighting the need to engage task-related strategies appropriately, which may be regulated through interactions with the VAN as seen in this thesis.

The second finding identifying the motor cortex as important in maintaining states important for task performance involved a seed-based functional connectivity analysis that identified connectivity between the lingual gyrus and the motor system as significantly related to autistic traits in a neurotypical sample. Crucially, this connectivity modulated the relationship between autistic traits and thinking in words, which was in turn linked to improved task performance in the 1-back specifically. This result suggests that thinking in words is an adaptive strategy for 1-back task performance, perhaps through the utilisation of short-term working memory (D. M. Williams et al., 2012), that is elevated in individuals with higher levels of autistic traits in both tasks regardless of whether this strategy was beneficial. The modulating effect of visual-motor connectivity on this relationship meant that it was specific to individuals with high connectivity between these regions. This coupling to vision could link task strategies directly to incoming visual input, enabling them to be maintained. This sort of visuomotor coupling has been shown to occur during task performance and is

thought to be essential for visuomotor behaviour (Ledberg, Bressler, Ding, Coppola, & Nakamura, 2007). The increased resting state connectivity between visual and motor regions may represent a tendency for this sort of external task-specific state maintenance, with the consequence that it may be engaged even when it isn't needed. Taken together these results suggest a role for the motor cortex in external state maintenance that is related to effective task performance, while highlighting the need for more general processes that enable these states to be maintained in a flexible manner in line with task demands.

7.3.1.3 Context Regulation

Context regulation describes the observation that participants maintain states differently depending on the external context. Previous research has shown that participants consistently engage in more 'mind wandering', or maintain more internal states, during tasks that are easy than those that are hard (Konishi et al., 2017; Levinson et al., 2012; Poerio et al., 2017; Rummel & Boywitt, 2014; Sormaz et al., 2018), a result that was reproduced in this thesis. This ability to regulate thoughts is important for limiting the negative consequences: mind wandering during external task performance leads to errors (Engle & Kane, 2004; McVay & Kane, 2012a) and has been shown to be a major component of poor performance on exams (Mrazek et al., 2012; Smallwood, Fishman, et al., 2007) and tasks in daily life (Kane et al., 2007; McVay et al., 2009).

There has been a debate in the literature about whether context regulation involves related processes (McVay & Kane, 2010; Smallwood, 2013a): maintaining external task states and internal states could be two distinct abilities with distinct mechanisms. This is closely linked to the debate on the role of executive control, as these resources could be used in maintaining external states exclusively (McVay & Kane, 2010, 2012b) or could be shared across internal and external states (Smallwood, 2010, 2013a). One recent study found that lesions in the lateral cortex were related to decreased processing related to both internal and external attention, suggesting overlapping processing (Kam et al., 2018). Another found that adjacent, but non-overlapping, regions in parietal cortex processed internal and external attention (Sestieri et al., 2010), again suggesting some related mechanism. By using MDES during two separate tasks that vary in their demands, and particularly by

simultaneously collecting fMRI data, this thesis found that there are shared resources between internal and external state maintenance related to executive control processes centred on the VAN.

7.3.1.3.1 The Ventral Attention Network

In both contrasts probing neural signals, whether reflecting in-the-moment activity or intrinsic architecture at rest, to identify those that were related to off-task thought in the 0-back and on-task in the 1-back, the VAN was found to be significantly related to this pattern of context regulation. In a seed-based analysis, the functional connectivity of the VAN to the motor cortex was significantly related to this pattern of thought, with participants that showed high connectivity showing greater off-task thought in the 0-back and greater on-task thought in the 1-back. Participants with low connectivity showed no difference between the two tasks along this dimension of thought. Similarly, in the scanner, moments where participants answered that they were engaging in off-task thought in the 0-back and moments where they were on-task in the 1-back were both related to activity in the DLPFC. This region is within the VAN as characterised by Yeo and colleagues (Thomas Yeo et al., 2011), the parcellation that was used in the earlier seed-based analysis.

The VAN has long been distinguished from the DAN by its activity profile: while the DAN transiently responds during moments of attention, the VAN shows sustained activation during task sets suggesting a role in their maintenance (Dosenbach et al., 2008; Dosenbach et al., 2007). The DLPFC in particular has a connection profile that has lead researchers to suggest a role in overarching control processes (Badre & Nee, 2017), such as the monitoring of information that enters working memory, as it is connected strongly to both sensory and memory related systems (Petrides, 2005). Research in humans has shown that it plays a role in the assessment of signals from internal and external sources during complex decision-making (Jiang et al., 2018), and lesions to this area lead to the absence of signals related to both internal and external attention (Kam et al., 2018). In this thesis, an analysis probing network interactions within this region showed results that were in line with this function: the functional interaction of task-related signals with those from the DMN in this region, as well as the cortical thickness of regions related to task-related signals, were both important in allowing internal states to be maintained during the 0-back. Taken together, these

findings suggest that the ability to monitor information entering working memory (Petrides, 2005) has been co-opted in humans to allow the prioritisation of internal states when the environment lacks a compelling goal. The external context may be incorporated into a 'gate' that alters the extent to which external and internal signals are weighted when they compete for global resources (Badre & Nee, 2017). This is also consistent with the role of this network is in the processing of biological salience (Seeley et al., 2007), which involves monitoring the environment in order to guide behaviour. It has been shown that particularly salient events are processed during internal states along with the ability to switch state (Kam et al., 2013), meaning salient events can highjack internal states during moments of particular environmental challenge, potentially via this network. This role is vital for effective context regulation in a dynamic world, allowing states to be maintained in line with external demands while continuously monitoring for meaningful changes.

7.3.1.3.2 Executive Control

This thesis provides several findings that suggest that executive control processes are involved more generally in state maintenance (Smallwood, 2010, 2013a; Smallwood & Schooler, 2006), rather than being unique to external states (McVay & Kane, 2010). The connectivity between the VAN and the motor cortex that was related to context regulation was also correlated with task performance across both tasks. This suggests that mechanisms that allow internal states to be maintained when the demands of the task are low can simultaneously be related to improved task-related processing. This pattern of connectivity may reflect the ability for task-related processes in the motor cortex to be deployed more effectively and appropriately. Close links to the motor system are essential for the types of behavioural adaptation known to be regulated through regions in the VAN (Menon & Uddin, 2010), and the ability to maintain internal states when task demands are low while still improving task performance suggests superior control in these participants. Additionally, the DLPFC region identified as involved in context regulation is often found to be involved in executive control processes, as shown by a tool for large-scale meta-analysis (Yarkoni et al., 2011). These results provide evidence for a role for executive control processes in maintaining states that is shared between internal and external states.

Taken as a whole, the results in this thesis further our understanding of a range of processes involved in maintaining specific states, as well as several that are involved more generally in state maintenance in line with environmental demands. The DMN was shown to play a role in determining state contents through coupling to regions involved in external processing, and these analyses suggest that the segregation of signals related to the task and vision from those in the DMN and other higher order networks is essential for allowing internal states to be maintained (Margulies et al., 2016; C. Murphy, Wang, et al., 2019). The motor cortex was shown to play a role in maintaining external states related to task performance, and by coupling to the VAN it allows participants to maintain these states in a manner that takes into account task context. This process of context regulation also engages the DLPFC (in the VAN) in-the-moment, possibly due to the ability of this region to monitor the allocation of resources in a way that takes into account the external context (Badre & Nee, 2017; Jiang et al., 2018; Petrides, 2005). Importantly for debates in the literature (McVay & Kane, 2010; Smallwood, 2010, 2013a; Smallwood & Schooler, 2006), executive resources seem to be recruited during both internal and external states, as shown by the association between the DLPFC and executive processes in a large-scale meta-analysis (Yarkoni et al., 2011).

7.3.2 States: Transitions

While using two conditions allowed us to better understand state maintenance through the simple idea that some states, and therefore processes, will be more engaged in one task than the other, probing the processes involved in state transitions is more difficult. This is due to the fact that a snapshot of a state taken using fMRI or experience sampling is less likely to capture a state in transition. This is partly due to the fact that theoretically less time is spent transitioning between states, and partly because these methods, particularly MDES, capture indirect measures of processing that are biased towards providing static answers. This paradigm leverages the knowledge that a specific task-driven external state is engaged at the moment of task performance to attempt to unravel the effect of time on ongoing thought, and better understand the systems engaged during state transitions. This section will elaborate the findings about these systems, starting with analyses that suggest that the DAN is involved in transitions between internal and external states. Next, it will describe how connectivity linked with these gradual transitions related positively to measures of

executive control, suggesting they are not a result of executive failure (McVay & Kane, 2010; Smallwood, 2010, 2013a; Smallwood & Schooler, 2006), while pointing out that another finding suggests that the earlier phases of transitions may relate negatively to aspects of executive control. It will finish by using the activity-related temporal analysis in the final experimental chapter as an example of how whole-brain approaches to understanding dynamics provide a fruitful avenue for better understanding the movement of the brain through state space.

7.3.2.1 The Dorsal Attention Network

A whole-brain seed-based analysis found that the DAN was involved in transitions from external to internal states. In a contrast looking for the effect of time on ongoing thought, participants with increased connectivity between the DAN and a region in the lateral occipital cortex showed a pattern of increasing off-task thought over time. Participants with low connectivity between these regions failed to show this pattern. There are two interesting details to this finding: firstly, it was unrelated to condition, and secondly, it showed positive relationships to both creativity and fluid intelligence. Together, these findings suggest that the DAN is involved in transitions to internal states in a manner that is unconstrained by external context and does not represent executive failure (McVay & Kane, 2010), but instead is a marker of improved intelligence and creativity. The DAN is predominantly identified in studies of external attention, and is shown to be transiently active during task performance (Corbetta et al., 2000; Corbetta et al., 2008; Corbetta & Shulman, 2002; Dosenbach et al., 2008; Dosenbach et al., 2007). Results from this literature suggest a role in goal-directed attentional processing (Corbetta & Shulman, 2002) that is highly consistent with a role in state transitions. Understanding internal and external states as two sides of the same coin, it holds that the functional architecture of this network would be related to transitions between states, as this result can also be interpreted as the ability to return to an external task state that allows for an increased tendency to drift to an internal state over time. This is perhaps more likely given that an analysis of brain activity in this thesis found that the DAN is active during on-task states, and also decreases in activity over time when assessed at each subsequent non-target. The fact that this result did not vary by task context is somewhat surprising given the fact that the continuous monitoring during the 1-back effectively requires external states to be maintained in this task (see Limitations). However, viewing the brain as a complex

interaction of large-scale networks points to the involvement of multiple systems in ongoing thought dynamics (Christoff et al., 2016). The DAN appears to play a role in state transitions between internal and external states irrespective of external context, which may be regulated by another network (for example, the VAN).

7.3.2.2 Executive Control

In addition to the finding that connectivity related to transitions to internal states over time was positively related to fluid intelligence and creativity, an analysis looking at cognitive correlates of ongoing thought found that differences in the ability to inhibit previously relevant information, measured during a task-switching paradigm (Mayr & Keele, 2000; Whitmer & Banich, 2007), is related to the levels of detail and the off-task nature of thoughts immediately following task performance. Specifically, participants who were better able to inhibit a task set that was recently relevant but no longer is were more on-task and detailed immediately following task performance across both conditions. This is particularly of note given the fact that the majority of effects related to state transitions in this thesis involved gradual shifts over relatively long periods of time. This result may provide the clearest insight into the processes that initiate state transitions, which are often the hardest to understand given the covert nature of ongoing thought (Smallwood, 2013a). This finding seems to imply that some aspects of executive control are recruited to maintain on-task states irrespective of task context (McVay & Kane, 2010), at least for limited periods of time. This finding provides a clear justification for theoretical frameworks that separate ongoing thought into moments of initiation and maintenance (Smallwood, 2013a). Initial thought initiation may be related to executive failure, with resources then being engaged to isolate the new state. However, it may additionally be necessary to distinguish moments of thought initiation from gradual transitions that appear to occur over longer periods of time, and relate more positively to executive control. Research using neuroimaging methods with greater temporal resolution may be necessary to unravel this complex relationship.

7.3.2.3 Whole Brain Dynamics

Both the seed-based connectivity and activity-based state analysis are limited in their ability to understand state transitions due to the fact that they provide static measures of the brain and relate them to experience. Additionally, they are biased towards finding single regions, or clusters, of activation or connectivity. This is due to

the cluster correction approaches that are most popular in fMRI analysis, and are necessary to control for the large numbers of comparisons that are carried out and, if left unchecked, lead to large numbers of false positives (Eklund et al., 2016). The whole-brain temporal activity analysis attempted to overcome these limitations by modelling time as a predictor of fMRI activity, to identify regions that varied over time with each uninterrupted non-target trial. It then plotted these whole-brain patterns of activity that relate to time in terms of their relationship to large-scale neural hierarchies (Margulies et al., 2016). The brain was found to functionally reorganise along multiple hierarchies over time: away from regions involved in visual processing towards motor regions, and away from regions involved in external task performance (Duncan, 2010) towards the DMN. Movement along this second hierarchy was found to positively relate to the rate of change towards off-task thought over time. These results show that, while single regions or networks may play important roles in ongoing thought dynamics, state transitions involve whole-brain reorganisations, and these can be meaningfully interpreted as changes along specific axes rooted in the intrinsic architecture of the cortex (Margulies et al., 2016). The gradient which predicted off-task thought in the analysis in this thesis is highly similar in structure to a dimension of brain organisation that was found to be engaged during task performance and disengage at rest using a different decomposition technique in another study (Shine et al., 2019). Taken together, these findings suggest that state transitions involve movement of the brain through a low dimensional space that may be predetermined by the brain's resting architectural principles. This approach is a novel and useful way to understand neural processing that is less biased towards identifying single regions, a methodological bias that may have led to an overly modular understanding of the brain (Heller, Stanley, Yekutieli, Rubin, & Benjamini, 2006).

Overall, these results points to a role for the DAN in transitions between internal and external states that is an extension of its known involvement in goal-directed external attention (Corbetta et al., 2000; Corbetta et al., 2008; Corbetta & Shulman, 2002; Dosenbach et al., 2008; Dosenbach et al., 2007). Connectivity in this network linked to gradual transitions to internal states was positively related to fluid intelligence and creativity in a way that adds to the complex literature on the relationship between ongoing thought and executive function (McVay & Kane, 2010; Smallwood & Schooler, 2006). It further suggests that transitions to internal states cannot be exclusively

understood as related to executive failure (McVay & Kane, 2010). The finding that inhibition relates to on-task thought immediately following task performance across both conditions highlights the need to separate moments of thought initiation from state maintenance (Smallwood, 2013a). It goes further to suggests that transitions in the early stages of state initiation may involve distinct processes than gradual changes, and may relate to different measures of executive control in a dissociable way. Finally, a whole-brain temporal analysis suggested that while traditional fMRI analyses involving cluster correction provide useful information about neural specialisation, transitions in the brain over time involve whole-brain changes. These changes can be meaningfully understood in terms of low dimensional reorganisations that relate to intrinsic brain architecture (Margulies et al., 2016), and approaches such as these enable an improved understanding of state transitions (Shine et al., 2019).

7.3.3 Managing Maintenance and Transitions: the Role of Executive Control

This thesis advances the debate on the role of executive function in ongoing thought, suggesting it is needed for the maintenance of both internal and external states, but also highlighting the need to consider state transitions when discussing this relationship. Connectivity related to transitions to internal states was related positively to both fluid intelligence and creativity, suggesting these transitions are not only not a result of executive failure (McVay & Kane, 2010; Smallwood & Schooler, 2006), but that they can be a marker of improved executive control. The same measure of fluid intelligence was also significantly related to off-task thought differently across the two tasks, but only in a contrast that also included time since the last task event. Individuals who scored higher on Raven's Progressive Matrices (RPM) showed a pattern of off-task thought that increased in the 0-back compared to the 1-back. While this suggests that individuals with greater fluid intelligence provided more resources for internal states in a manner that depends on the task (Levinson et al., 2012; Rummel & Boywitt, 2014), it also suggests that this increases over time. This result further adds to the complex literature on this relationship (Engle & Kane, 2004; Kane et al., 2007; Levinson et al., 2012; McVay & Kane, 2009, 2010, 2012a, 2012b; McVay et al., 2009; Mrazek et al., 2013; Mrazek et al., 2012; Robison & Unsworth, 2015; Rummel & Boywitt, 2014; Smallwood, 2010, 2013a; Smallwood et al., 2002; Smallwood & Schooler, 2006; Smeekens & Kane, 2016; Unsworth & McMillan, 2013; Unsworth &

Robison, 2016) and suggests that transitions to internal states over time are positively related to executive function, specifically in tasks with low levels of external demands. Identifying tasks that require limited external processing and flexibly transitioning between internal and external states may be a mark of fluid intelligence. This is in line with several recent findings from both the fMRI and experience sampling literature. First, a previously mentioned study that identified whole-brain reorganisations during task performance found that individuals who scored higher on the same measure of intelligence (RPM) engaged a task-related whole-brain state more during task performance and disengaged it more during rest over similar time periods to in the analysis in this thesis (Shine et al., 2019). A second study using experience sampling found that participants with higher executive abilities had greater task-unrelated thought variability (Welhaf et al., 2019). This meant that they engaged in a greater range of internal states characterised by varied content as well as shorter length, with more transitions back to task performance. Taken together, these results suggest that the ability to appropriately transition between internal and external states is a marker of improved executive function, and that intelligent people utilise these abilities to more efficiently perform tasks while also engaging in internal states. This ability is an extension of context regulation, but shows a more nuanced relationship to executive control that may have been missed in studies not including dynamic analyses.

Taken as a whole, the results of this thesis provide clarity on the contentious theoretical point regarding the role of executive resources during internal states (McVay & Kane, 2010; Smallwood, 2010, 2013a; Smallwood & Schooler, 2006). Viewing ongoing thought in terms of states, they imply that executive resources are required for the maintenance of both internal and external states in a manner that is regulated in line with external demands through processes within the VAN. Connectivity profiles related positively to gradual transitions to internal states were correlated with creativity and fluid intelligence, while early moments of state transition related to inhibition in a way that suggested improved abilities were related to staying temporarily on-task. Gradual allocations of resources to internal states over time may coincide with whole-brain reorganisations along multiple functional hierarchies rooted in intrinsic brain architecture (Margulies et al., 2016). Individuals with better executive function were more able to manage these transitions in line with the demands of the external task, identifying when limited time needs to be spent in external states and

engaging these transitions more effectively (Shine et al., 2019; Welhaf et al., 2019). Fundamentally, this thesis suggests that viewing internal states as a result of executive failure is an incomplete understanding (McVay & Kane, 2010; Smallwood, 2010, 2013a; Smallwood & Schooler, 2006), and makes it clear that this complex relationship can only be understood when taking into account both external context and transitions that occur over different time-scales (Smallwood, 2013a).

7.4 The Role of the Default Mode Network

Due to the central position the DMN holds within the literature on ongoing thought, it is worth further clarifying what this thesis adds to the debate about the role of this network (Andrews-Hanna et al., 2014; Christoff et al., 2016; Margulies et al., 2016; R Nathan Spreng, 2012). This network was not identified in whole-brain analyses linking brain networks to off-task thought, instead it was predominantly found relating to the level of detail in participants' thoughts in a manner that was stronger in the 1-back task. This replicates previous studies using similar datasets that have found the DMN to be linked to task-related detail both in terms of functional connectivity (Vatansever et al., 2018) and activity (Sormaz et al., 2018). The interaction of this network with regions involved in external task performance and visual input was shown to be important for determining state contents in several analyses. These findings may appear surprising given the almost synonymous nature in which the DMN and off-task thought are talked about in parts of the literature (Andrews-Hanna et al., 2014). However, several authors have called for this association to be relaxed (Christoff et al., 2016; R Nathan Spreng, 2012), supported by a range of studies that identify the DMN as active during external task performance. This is particularly true in studies of social cognition (Mars et al., 2012) and memory-guided task performance (Konishi et al., 2015; C. Murphy et al., 2018; C. Murphy, Wang, et al., 2019; Smallwood, Tipper, et al., 2013), but also extends to studies on task-switching (Crittenden et al., 2015; V. Smith et al., 2018) and "automated" processing (Esterman, Noonan, Rosenberg, & DeGutis, 2013; Vatansever et al., 2017). A study using 6 tasks (some requiring internal and some external attention for performance) found that the DMN coupled to task-specific regions during all 6 tasks in a manner that related to improved performance (Elton & Gao, 2015). The DMN includes many hub regions (Tomasi & Volkow, 2011), with far-reaching connections to many other networks allowing for multimodal processing (Bonner, Peelle, Cook, & Grossman, 2013), and is highly metabolically

active (Leech & Sharp, 2014). It has also been shown to contain information about signals in the rest of the brain (J. M. Kernbach et al., 2018), and is positioned at the top of a cortical hierarchy that suggests a role in abstract, integrative processing (Margulies et al., 2016). Finally, it is well protected within the brain from ischemic stroke and abnormalities within this network can be identified in a range of neurological disorders including Alzheimer's disease, schizophrenia, ASD, depression, and ADHD (Leech & Sharp, 2014). Taken as a whole, these findings suggest a highly domain general role in coordinating cognitive functioning that is necessary for off-task thought but not specific to these states. Theories have been proposed that link the DMN to coding general arousal and attention (Leech & Sharp, 2014), with others suggesting it integrates spatial, self-referential, and temporal information to encode scenes (V. Smith et al., 2018). This is supported by evidence that this network encodes information over longer time periods, shown by a relationship to coherent rather than incoherent narratives (Tylén et al., 2015). A hierarchical model of the entire central nervous system places the DMN at 'level 7', which has a proposed role in regulating lower levels of the hierarchy based on conceptual interpretations of perceptual input that are in turn based on past experience (R. Smith et al., 2017). While the experimental setup used in this thesis is not specifically designed to answer questions about the role of the DMN, the involvement of this network in the level of detail in thought, and the consistent finding that coupling this network to regions relating to perceptual input and task-related thought is important for defining state contents is in line with this type of function, especially when considered alongside studies showing a clear role in memory-guided cognition (Konishi et al., 2015; C. Murphy et al., 2018; C. Murphy, Wang, et al., 2019; Smallwood, Tipper, et al., 2013). The results of this thesis are further evidence that this network should not be considered 'task-negative' or specific to off-task thought.

7.5 Limitations and Open Questions

While each experimental chapter includes limitations to the specific analyses used, there are several general limitations that are important to acknowledge when discussing the overall implications of this thesis. These also leave some open questions that will need to be answered by future research. The first is that the results are likely to be related to the specific nature of the paradigm, both in terms of the components identified and the neural systems involved. This paradigm requires spatial

decision-making about the location of simple visual information. This means that the specific states induced by the task as well as by the change in condition are likely driven by these conditions. For example, the off-task component identified was loaded highly on self-related and other-related thought. This is more likely to be the case given the fact that the task did not require processing related to these types of content. Similarly, the identification of a modality component may be driven by the fact that the 0-back can be done visually, but the 1-back seems to involve a strategy that is mediated by verbal working memory. The fact that similar components are identified in daily life gives some confidence that they represent dimensions of experience that are valid in the real-world (Ho et al., 2020). However, there are important differences, such as the fact that the task focus question loads less strongly in real-world settings, possibly driven by the fact that tasks performed over the course of a normal day require a range of different processes that would score highly across the 13-questions asked. This should be held in mind when interpreting the results from this thesis: these components are not meant to define the "true" structure of ongoing thought. They are merely supposed to find a multidimensional state space that can be probed to better understand the neurocognitive systems involved in maintaining and transitioning within this space. Relatedly, the findings relating to these processes will be affected by the specific nature of the paradigm. The consistent identification of the visual systems involved in task-related detail is likely given the visual nature of the task. Work in this lab currently is attempting to determine the generalisability of these components, using a similar MDES approach across a range of tasks and movie-watching conditions (Konu et al., in prep.). Findings from these experiments suggest that, while there is some conserved structure to thoughts, the tasks used do have a significant effect on the components that are found by PCA: for example, the use of a self-other task increases variance along this dimension and causes a component that separates these questions to be identified. Future research should continue to extend these approaches to a range of tasks that each place different boundary conditions on the states that will be engaged during task performance, using a range of modalities and processes. Naturalistic movie-watching approaches may provide the best real-world approximation that can still leverage known locations in state space to enable an understanding of the way the brain moves through this space (Vanderwal, Eilbott, & Castellanos, 2019).

The second open question relates to the fact that processes identified as related to state transitions were predominantly found across both tasks. The relationship between the DAN and transitions towards internal states was identified in a main effect, as were changes in the brain over time following task performance. This is somewhat surprising given the fact that the 1-back was included to ensure continuous monitoring in this condition. It may be the case that neural mechanisms involved in state transitions are dissociable from those involved in ensuring states are maintained differentially across conditions, at least at the level of brain networks and over the time scales measured by fMRI. This is possible given the consistent identification of the DAN and VAN in different aspects of ongoing thought that vary by their involvement of a task contrast. However, it is important to note that there were no significant differences in thought dynamics across the two tasks, either in the laboratory (although there was a trend towards this effect) or in the scanner. Taken together with the fact that participants had a very high accuracy across both tasks this may suggest that the 1-back was too easy and could be performed somewhat automatically, especially given the repeated exposure over at least 3 days. Future research using a difficult comparison condition may allow the identification of processes involved in state transitions that are specific to the 0-back to be better isolated. The movement of the brain in state space defined in the final experimental chapter in this thesis can be tested simply in a range of tasks without the need for experience sampling, which both takes time and may alter ongoing thought in meaningful ways (see next point), to further examine the extent to which dynamics are context-dependent.

Experience sampling is also limited because it requires participants to self-report their own thoughts. While probe-caught methods are advantageous because they do not specifically ask the participant to monitor their thoughts, this requirement still makes participants aware that their thoughts are being measured in a way that may alter their current state (Smallwood & Schooler, 2015). Additionally, asking participants for their thoughts at a defined moment in time requires them to decide exactly what time period to choose and how long to consolidate over. Although participants are given the same instructions, this may introduce variance. It also may be biased towards identifying defined states at the extremes of state space (Karapanagiotidis, Vidaurre, et al., 2019), rather than transitions. As a whole, future

research will need to use covert behavioural indicators of participant state to enable a more thorough investigation of the brain's movement through state space without these limitations. Studies have shown that eye-tracking (Bixler & D'Mello, 2014, 2015, 2016; Bixler et al., 2015), pupilometry (M. S. Franklin, Broadway, et al., 2013; Kang et al., 2014; Konishi et al., 2017; Smallwood et al., 2011), heart rate and heart rate variability (Blanchard et al., 2014; Smallwood, O'Connor, et al., 2007), and skin conductance (Frith & Allen, 1983) are all indicators of state transitions. Combining these with measures of brain activity would provide additional information about the movement of the brain through state space that does not rely on experience sampling self-report.

Finally, the analyses in this thesis are temporally limited by fMRI, which in this case takes measurements of brain activity every 3 seconds. The results in this thesis relating to state transitions involve changes that emerge from around 5 to 30 seconds, and the use of fMRI limits results towards those in this time frame. Understanding state transitions on a finer timescale will require the use of brain imaging methods that are more temporally precise, such as EEG or MEG. Using these alongside similar MDES paradigms it may be possible to track the emergence of specific states in the early stages, giving insight into how they are ignited (Smallwood, 2013a) and how they gain entry into the global workspace (Kam & Handy, 2013; Smallwood, 2010). This may help to unravel further the complex relationship between executive control and the emergence of internal states, clarifying whether their initial occurrence is indeed related to executive failure in all or only some cases (McVay & Kane, 2010; Smallwood, 2013a).

7.6 Conclusion

In conclusion, the results of this thesis suggest that ongoing thought can be understood in terms of the movement of the brain through a low dimensional state space. This space can be defined along several axes by decomposition techniques such as PCA, which in this thesis identified four dimensions of experience: on- to off-task, vague to detailed, words to images, and positive to negative emotional valence. This space can also be understood as the movement of brain activity patterns along axes that relate to hierarchies rooted in the brain's functional organisation at rest (Margulies et al., 2016). Maintaining internal and external states in a manner that

accounts for the demands of the current situation involves the ventral attention network, which may have adapted its role in detecting biological salience (Seeley et al., 2007) to evaluate and provide information about the external environment so that states can be maintained in the most effective way. Transitions between internal and external states are related to the dorsal attention network, in line with a role in the goal-directed regulation of attention (Corbetta et al., 2000; Corbetta et al., 2008; Corbetta & Shulman, 2002; Dosenbach et al., 2008; Dosenbach et al., 2007). Executive control processes are engaged during both internal and external states, but this relationship can best be understood when taking into account transitions between states. Intelligent individuals are better able to manage these transitions to ensure the most effective allocation of resources between internal and external states over time in line with task demands (Shine et al., 2019; Welhaf et al., 2019). The default mode network is most strongly linked to the level of detail in thoughts, particularly through its relationship to perceptual regions. The coupling of the DMN to sensory regions is important for determining the contents of thought and decoupling the DMN from incoming perceptual details from the external world is necessary for internal state maintenance (Kam & Handy, 2013; C. Murphy et al., 2018; Smallwood, 2013b; Smallwood et al., 2011; Smallwood, Tipper, et al., 2013). These results are in line with a domain general role for the default mode network related to the coordination of both memory-related and perceptual information in order to determine state contents and guide cognition in concert with the rest of the brain and central nervous system (R. Smith et al., 2017). It is well placed to serve this function at the top of a neural hierarchy of multimodal integration (Margulies et al., 2016), providing it with information about signals in the rest of the brain (J. M. Kernbach et al., 2018). Future research should focus on extending this state space framework to a range of tasks, including naturalistic movie-watching paradigms (Vanderwal et al., 2019), in order to understand whether it is able to characterise real-world ongoing thought dynamics. It should also utilise behavioural markers that indicate participant state along with neuroimaging approaches with higher temporal resolution to better understand the movement of the brain through state space in real time.

Appendices

A.1 Supplementary Materials: Chapter 3
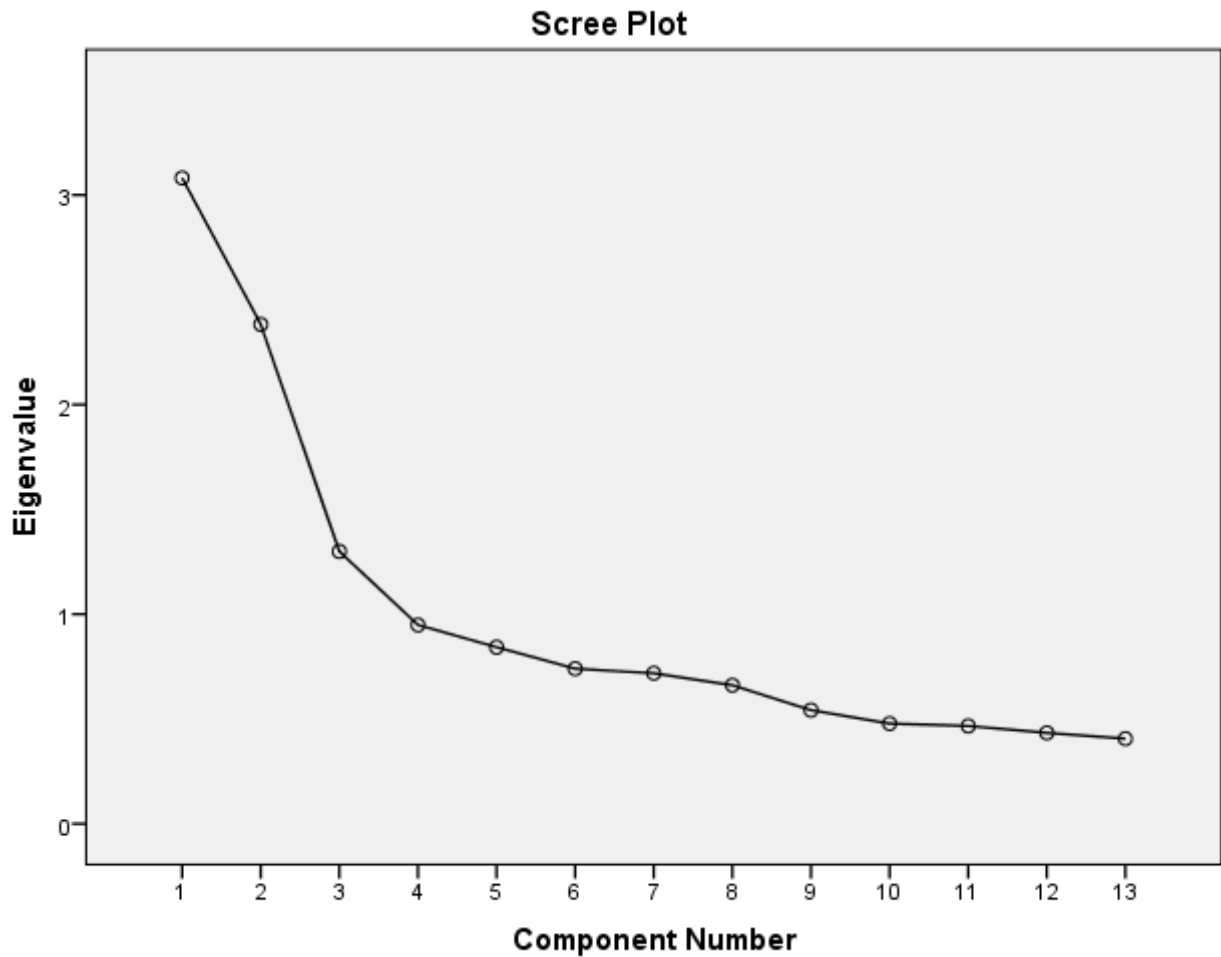
Figure S 1: Scree plot from PCA used to select number of components (4)

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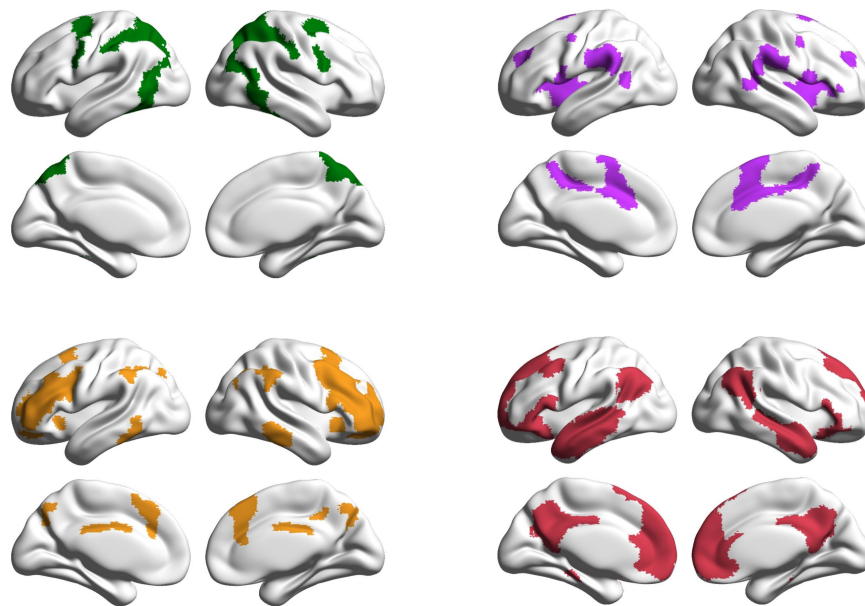
Figure S 2. Seeds for the (from top left clockwise) dorsal attention, ventral attention, default mode, and frontoparietal networks from Yeo and Krienen et al., (2011).

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).
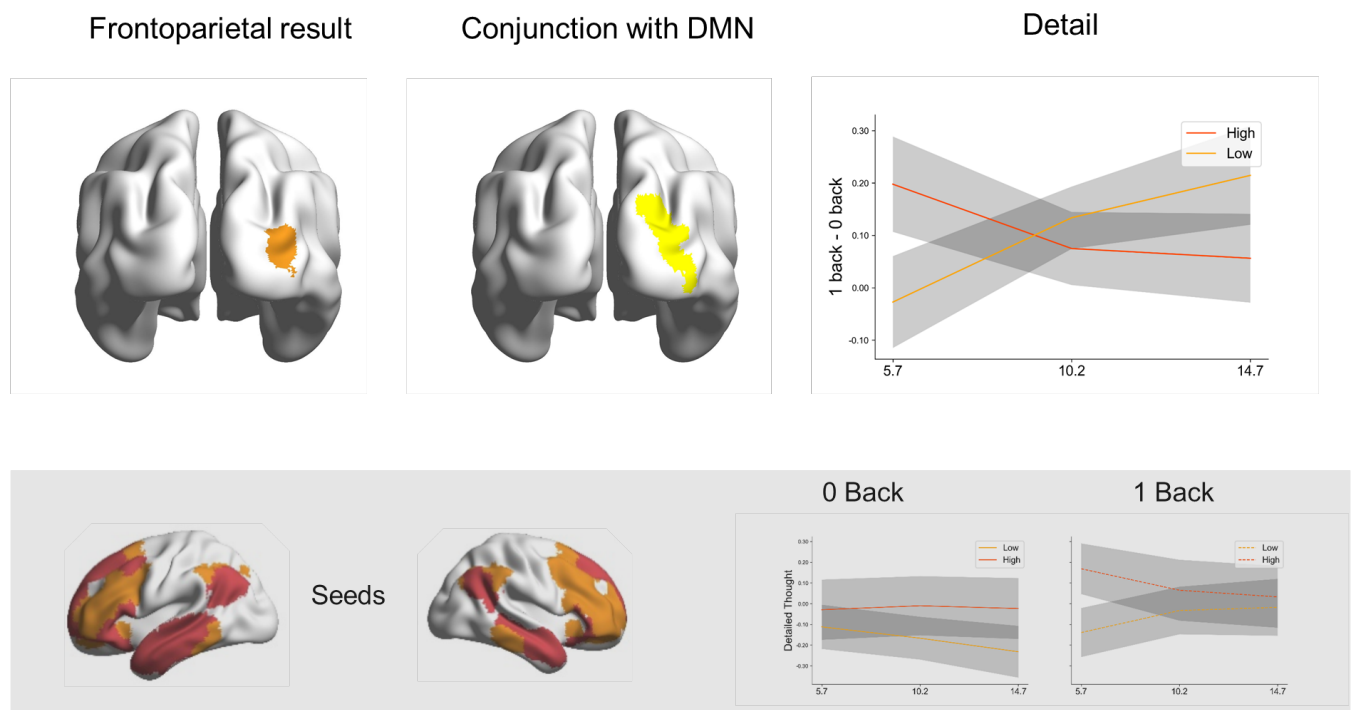
Figure S 3. Trend level fronto parietal network effects. Splitting the participants based on their patterns of connectivity revealed that strong connectivity was associated with greater detail in the 1-back task at earlier intervals while lower levels of connectivity was linked to patterns of increasing 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.

A.2 Supplementary Materials: Chapter 4

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
Detailed	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

Table S 1. Mind wandering questions asked to each participant during MDES. The first question was always "Task" then the other 12 questions in a random order. The scores from these questions were entered into a PCA.

Thought component	Contrast	Cluster size	p-value	MNI coordinates
Off-task	**Main effect on-task**	**411**	**.0043**	**(34, -60, 44)**
		367	**.0069**	**(-30, -70, 44)**
	0-back off-task, 1-back on-task	**198**	**.0308**	**(-26, 40, 30)**
Detail	Main effect negative detail	285	.0291	(-32, -48, 44)
		243	.0449	(-8, -62, 54)
	Detail in 1-back, negative detail in 0-back	222	.0258	(-8, -50, 22)
Emotion	Main effect positive emotion	726	.0001	(40, 16, -16)
		253	.0196	(-28, 24, -22)
Task contrasts	**Contrast**	**Cluster size**	**p-value**	**MNI coordinates**
	0-back>1-back	**7878**	**<.0001**	**(-8, -60, 10)**
		5397	**<.0001**	**(52, -30, 14)**
		4269	**<.0001**	**(-10, 64, 2)**
		545	**.0004**	**(36, -90, 0)**
		359	**.0039**	**(-14, 20, 2)**
		211	**.030**	**(4, -88, -16)**
		202	**.034**	**(-56, -30, 8)**
	1-back>0-back	**1160**	**<.0001**	**(-42, 2, 28)**
		880	**<.0001**	**(-28, -62, 42)**
		504	**.0007**	**(-4, -2, 56)**
		186	**0.0436**	

Table S 2. All significant clusters from the task-based analysis with multi-dimensional experience sampling. The primary analysis is shown in bold, the results from the other components are including from follow-up analyses.

Network 5 - 17 interaction					
Mask	Thought	Task	F-value	Equivalent r-value	Equivalence test p-value
DLPFC	Off-task	0	12.79	0.2942	Significant result: used to define effect size
		1	2.343	0.130612	0.018
	Detail	0	0.356	0.00263	0.001
		1	0.773	0.005693	0.003
	Modality	0	0.775	0.005708	0.003
		1	2.865	0.144403	0.03
	Emotion	0	0.551	0.004065	0.002
		1	0.281	0.045657	0.001
On-task regions (bilateral parietal)	Off-task	0	0.121	0.029925	0.001
		1	0.549	0.063641	0.002
Whole brain	Off-task	0	0.097	0.026796	<.001
		1	0	0	<.001
Network 10 -16 interaction					
Mask	Thought	Task	F-value	Equivalent r-value	Equivalence test p-value

DLPFC	Detail	0	11.229	0.277111	0.412
		1	14.014	0.306667	Significant result
	Off-task	0	7.145	0.2242	0.185
		1	6.440	0.213382	0.151
	Modality	0	0.563	0.097401	0.002
		1	1.293	0.097401	0.007
	Emotion	0	0.432	0.056478	0.002
		1	0.125	0.030415	0.001
On-task regions (bilateral parietal)	Detail	0	0.441	0.057062	0.002
		1	0.214	0.039783	0.001
Whole brain	Detail	0	0	0	<.001
		1	0.183	0.036793	0.001

Table S 3. Equivalence tests to check the specificity of the significant interactions identified within DLPFC. Effects that cannot be dismissed as null when looking for an effect of the size of our significant findings are in bold. The effect of the network 5 – network 17 interaction is specific to DLPFC and off-task thought in the 0-back. The effect of the network 10 – network 16 interaction is specific to DLPFC, but is similarly related to detail in both tasks, and may also relate to off-task thought as this test was not significantly equivalent to 0.
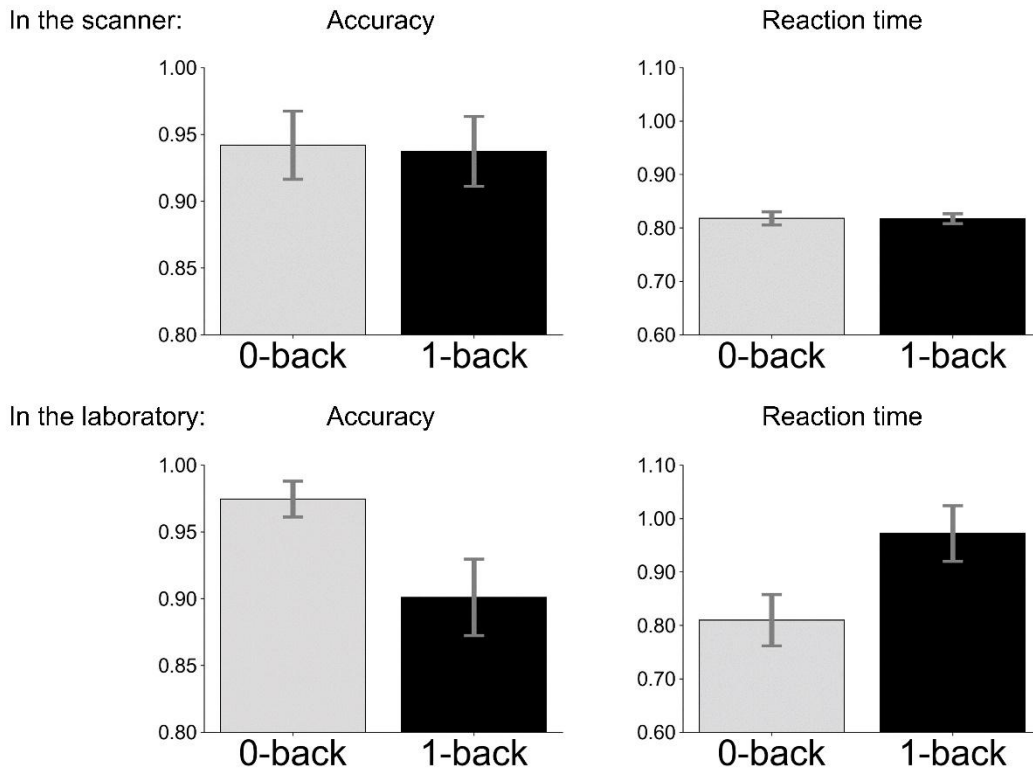
Figure S 1. Accuracy and reaction time in the scanner and laboratory during the 0- and 1-back tasks. Responses were significantly more accurate and faster during the 0-back in the laboratory, and there was no difference in the scanner.
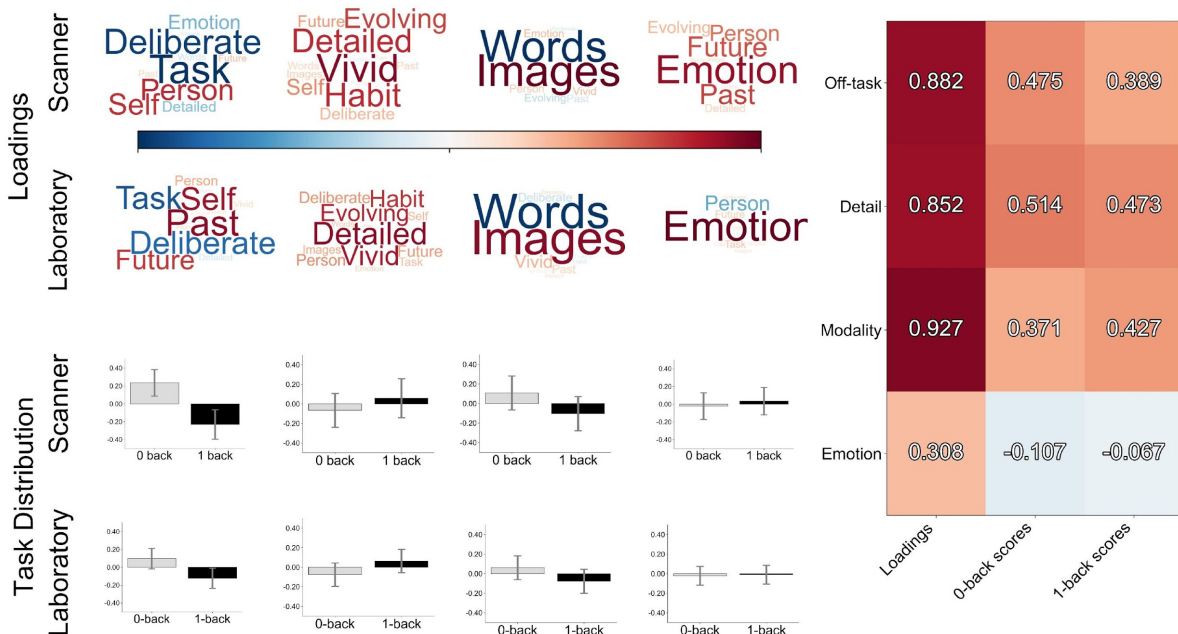
Figure S 2. PCA results characterised for scanner (n=60) and laboratory (n=146). Wordclouds show the loadings of each of the 4 components of thought (colourbar from

-1 to 1). The components were labelled as (from left to right) Off-task, Detail, Modality, and Emotion. Bar charts show the levels of these thoughts across the two tasks. Heatmap represents the similarity in (from left to right) loadings (across 13 questions), scores in the 0 back, and scores in the 1 back (across individuals).

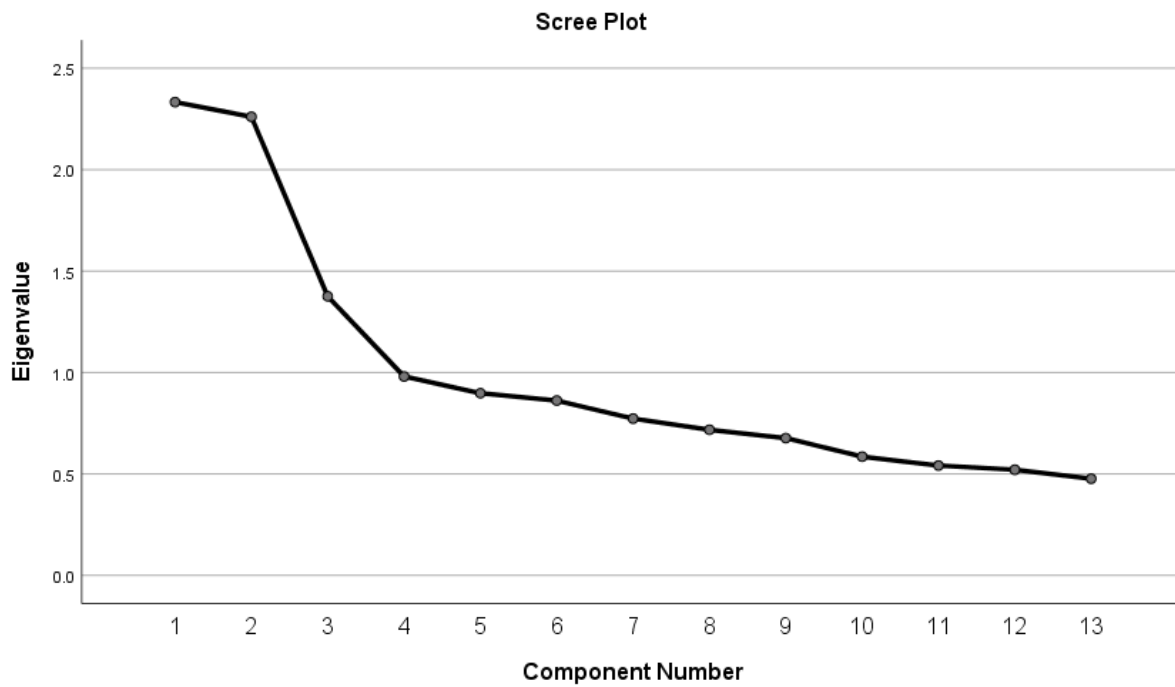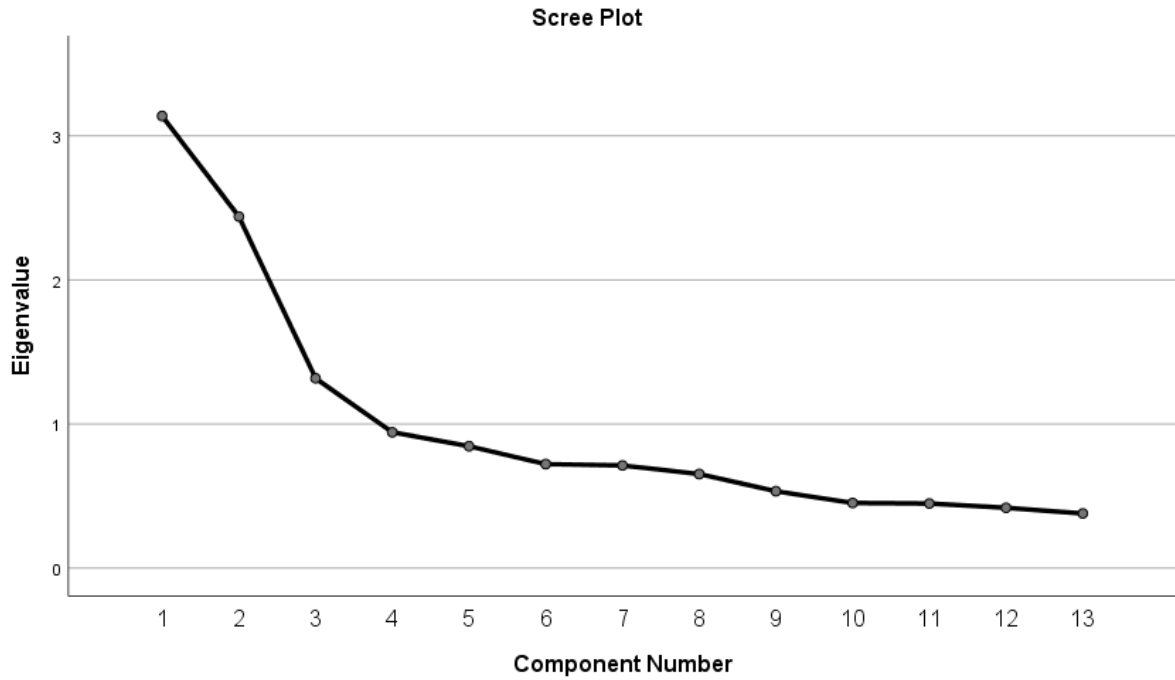Figure S 3. Scree plots showing the eigenvalues of the 4 components of thought. The sharp change in slope following component 4 was used to select on 4 components for further analyses in both the scanner (top) and laboratory (bottom).
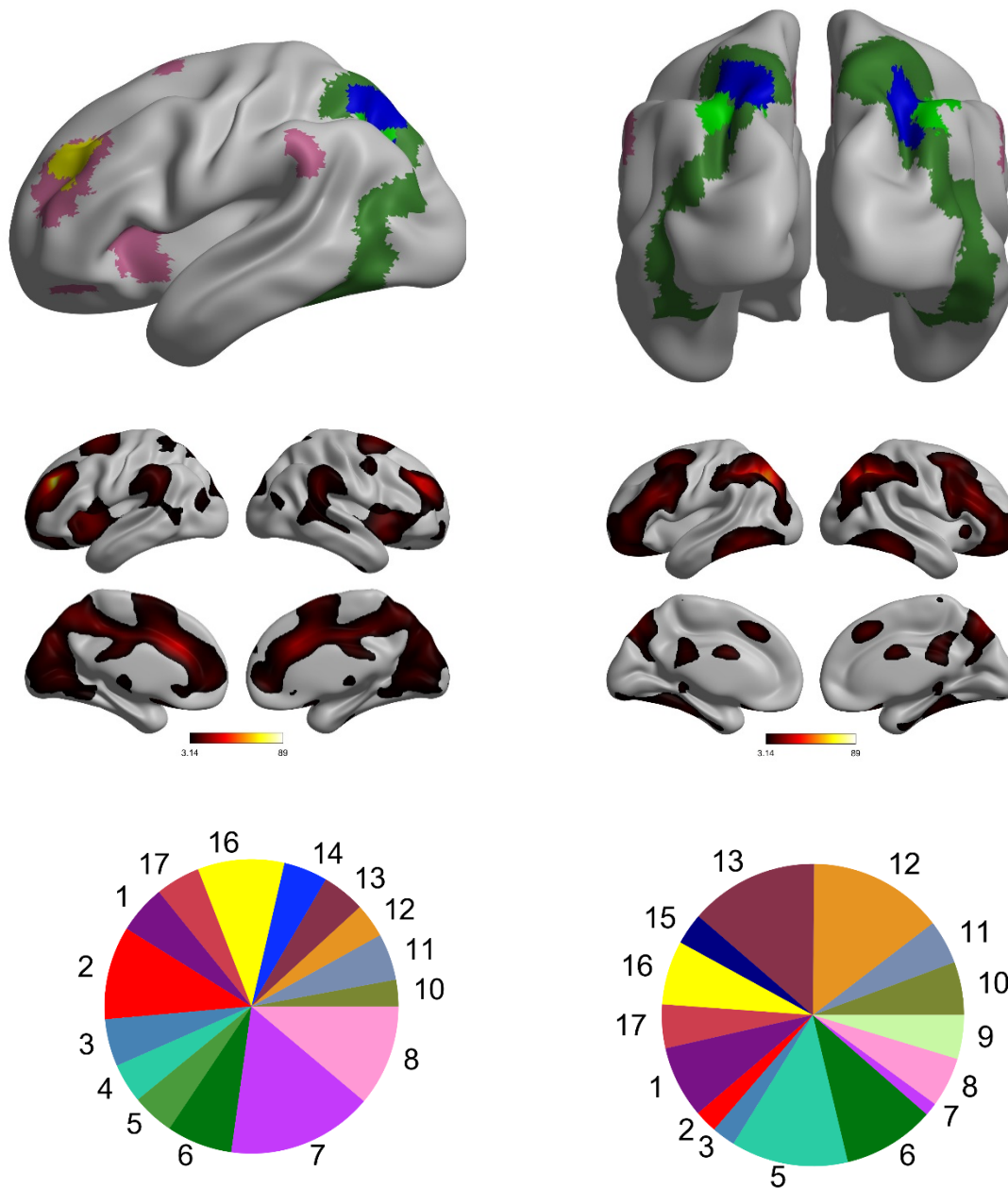
Figure S 4. Overlap of task-related regions with Yeo 17 networks, and pie charts showing the percentage of their resting state network that fell within each Yeo network[7]. The DLPFC region that was significantly more related to off-task thought in the 0 back and on-task thought in the 1-back fully overlaps (yellow) with Yeo 8 (pink), part of the Ventral Attention or Salience network. The bilateral parietal regions related to on-task thought in both tasks overlaps predominantly (blue, non-overlapping regions are shown in light green) with Yeo network 5 (dark green), which is part of the Dorsal Attention network. Similarly, the resting state connectivity of the DLPFC is predominantly in networks 7 and 8, making up the ventral attention network, while the superior parietal connectivity is largely in dorsal attention (5, 6) and frontoparietal control (12,13) networks.
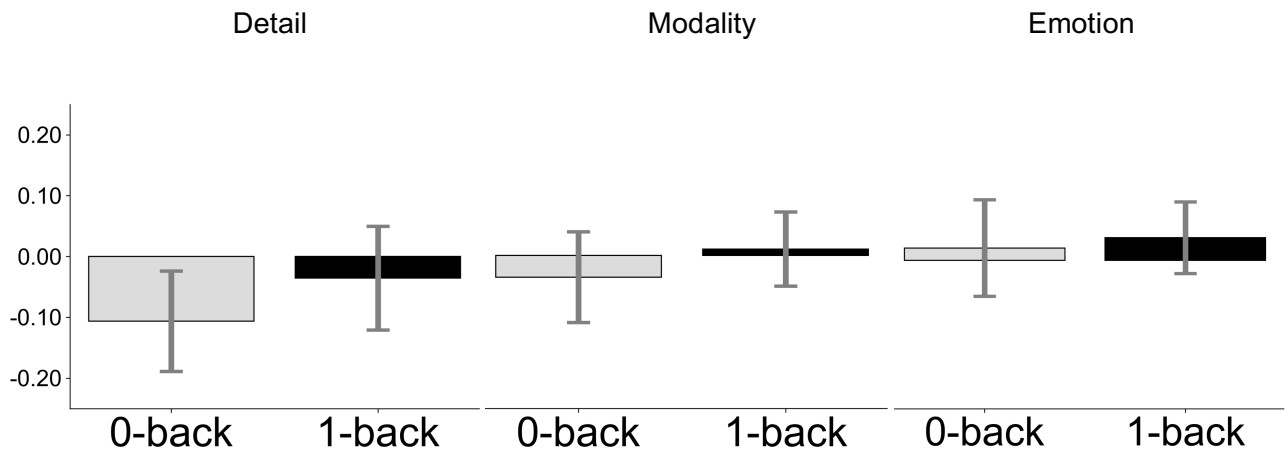
Figure S 5. Relationship of activity in the left DLPFC to the other components of thought. There was no task-dependent relationship (defined by the subtraction of the relationship in one task from the other) to any other component of thought, confirmed by equivalence analysis.
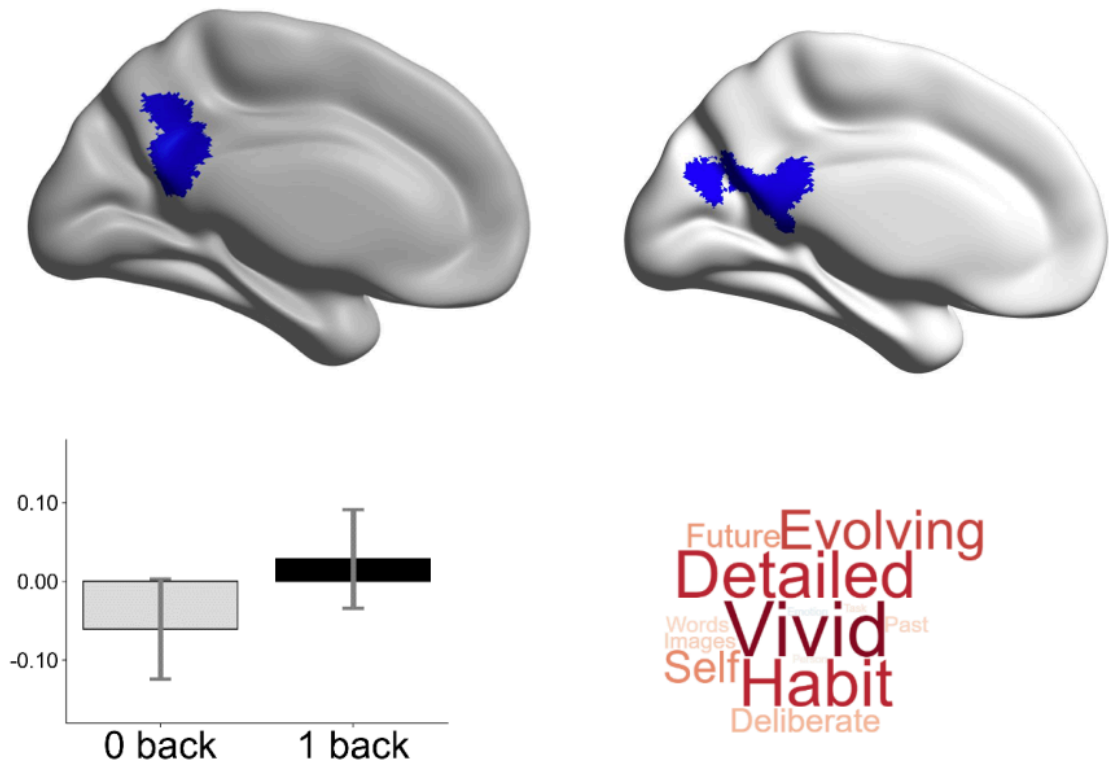
Figure S 6. Repeating the analysis with the other components of thought identified a region of the posterior cingulate cortex that was related to more detailed thought in the 1-back, and less detailed thought in the 0-back (top left). The association with detailed thought (wordcloud) in each task is shown in the bottom left. The brain on the top right shows an overlapping region of the brain that was identified as related to detailed thought in a previous study.
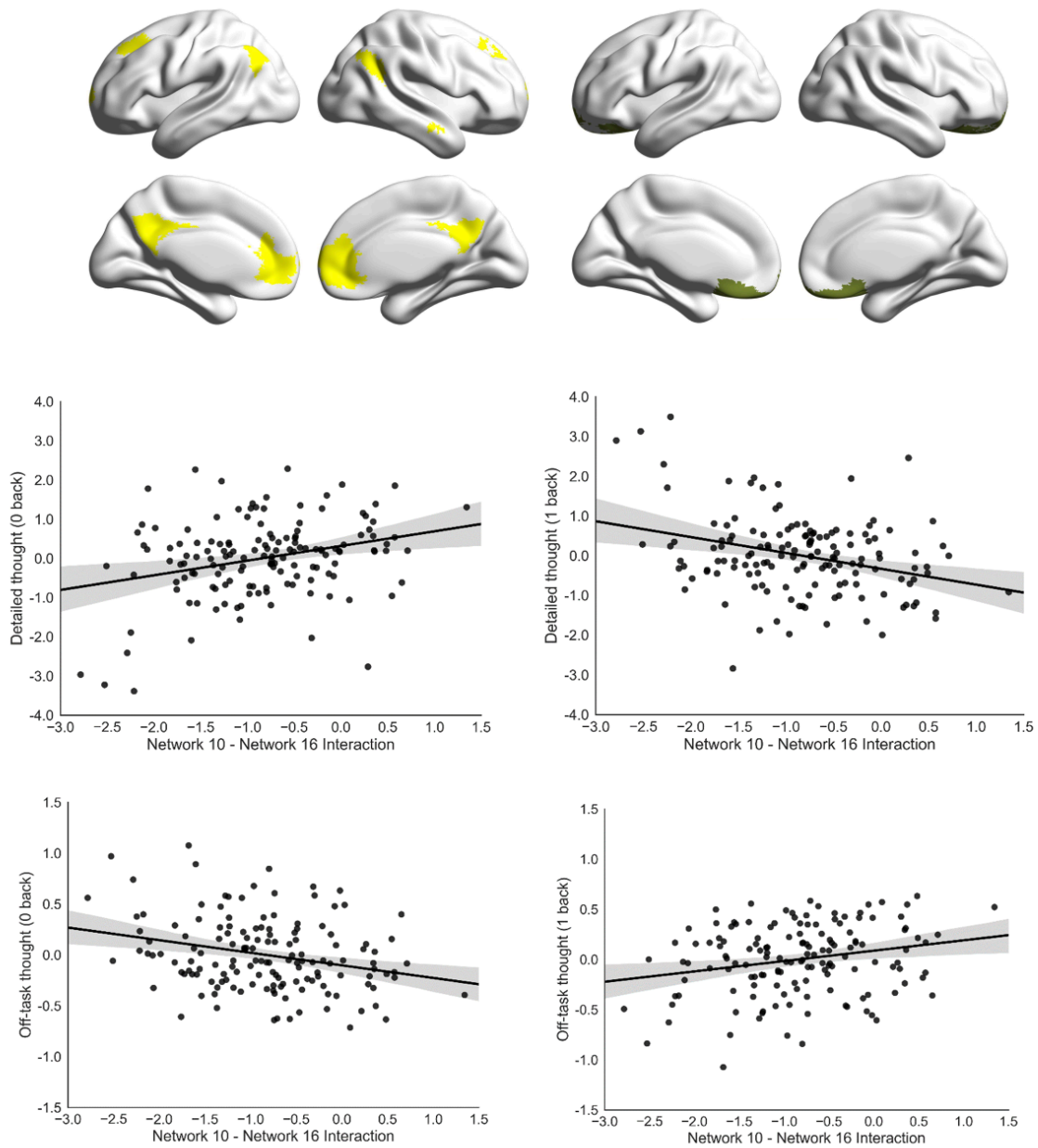
Figure S 7. The interaction between network 10 and network 16 within DLPFC is related to detailed thought in a task dependent manner. Stronger coupling between the network 10 and network 16 components within the DLPLC is related to more detailed thought in the 0-back, and less detailed thought in the 1-back. While not significantly passing Bonferroni correction, this interaction was also related to off-task thought with an effect size that could not be dismissed as null upon equivalence testing. This relationship is also task dependent, with the interaction negatively related to off-task thought in the 0-back, and positively in the 1-back. Network 10 is a region within the limbic system in vMPFC, and network 16 is the core of the DMN.
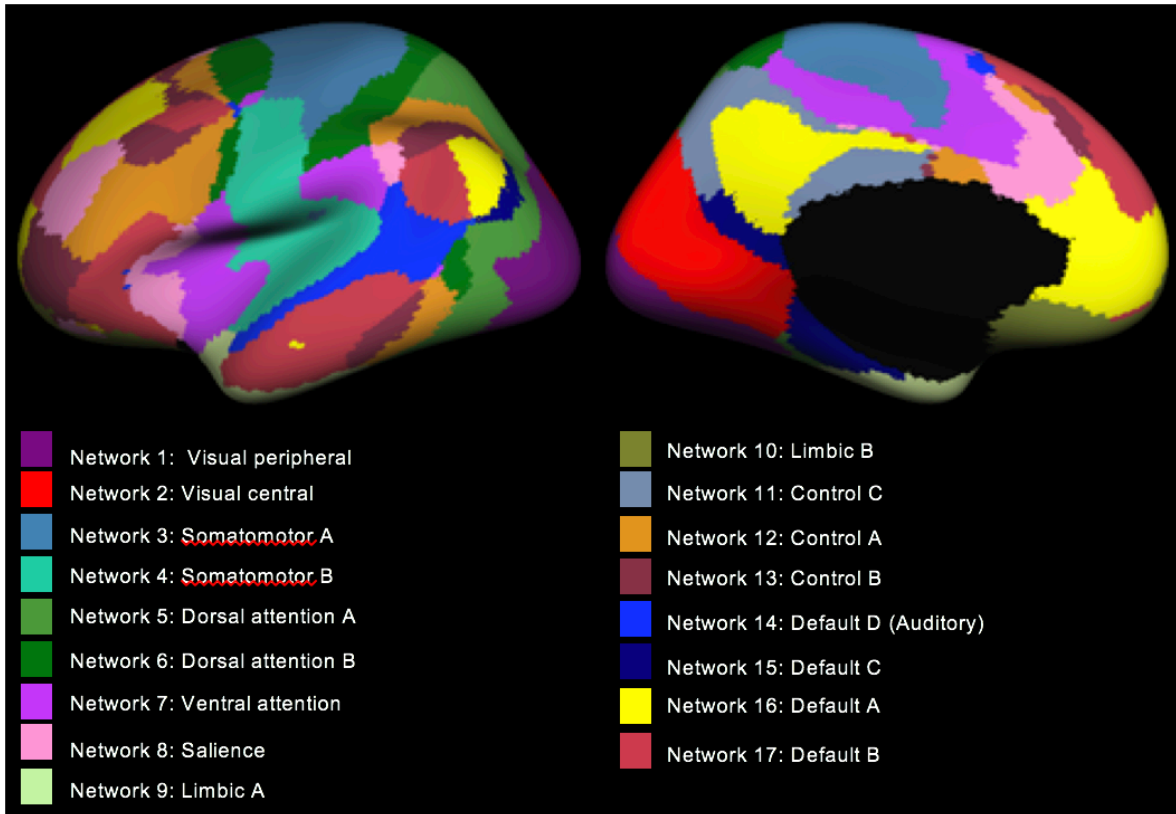
Figure S 8: Full description of the Yeo 17 networks. Names are taken from Baker, J. T., Holmes, A. J., Masters, G. A., Yeo, B. T., Krienen, F., Buckner, R. L., & Öngür, D. (2014). Disruption of cortical association networks in schizophrenia and psychotic bipolar disorder. JAMA psychiatry, 71(2), 109-118.
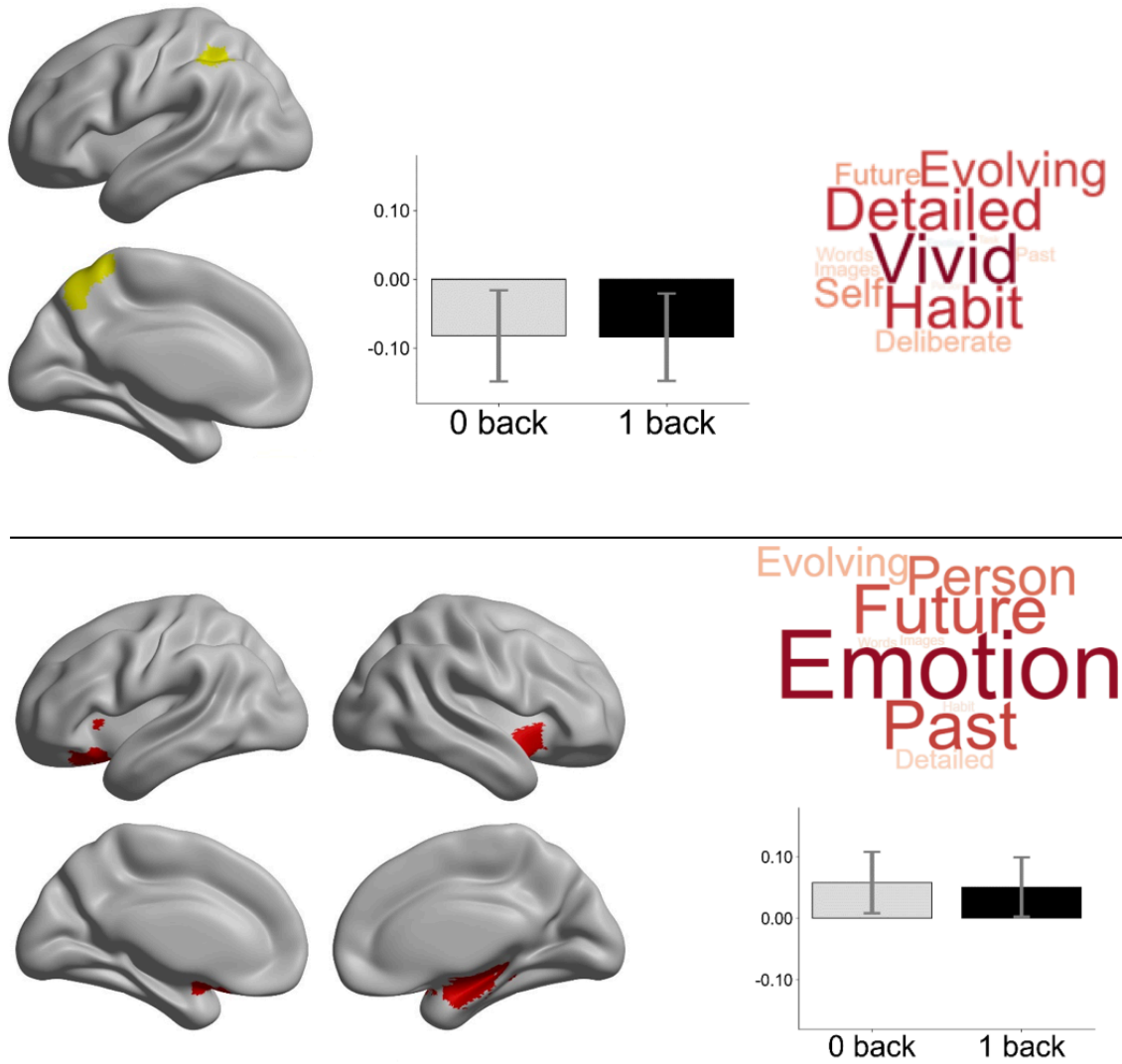
Figure S 9. No other results showed a pattern consistent with context regulation, but main effects identified brain regions related to vague thought (or negatively related to detail; top left) and positive emotional thought (bottom left).

A.3 Supplementary Materials: Chapter 5

Associated scale	Region	Size (vertices)	MNI coordinates (peak)
AQ Social	Left Lingual Gyrus	23	[-4.5, -75.9, 0.9]

Table S 1. Details of the significant cluster from the cortical thickness analysis after correction at a cluster forming threshold of Z=3.1, p<.05 FWE-corrected.

Associated scale	Region	Size (voxels)	MNI coordinates (peak)
AQ Total	Left Motor Cortex	297	[-44, -10, 38]
	Right Motor Cortex	362	[26, -10, 68]
AQ Imagination	Ventromedial prefrontal cortex	374	[12, 40, -26]
	Medial superior parietal lobule	283	[-12, -32, 54]

Table S 2. Details of the significant clusters from the functional connectivity analyses after correction at a cluster forming threshold of Z=3.1, p<.05 FWE-corrected. All analyses were performed using a seed with 6mm radius centred on the peak coordinates from Supplementary Table 2.

	AQ social	AQ imagination	AQ total	Mean detail	Mean off-task	Mean modality	Mean emotion	Detail difference	Off-task difference	Modality difference	Emotion difference

Left motor cortex connectivity	R	.238**	.333**	.318**	0.071	0.008	**-.212****	0.098	0.023	0.051	0.051	-0.023
	Sig.	0.002	0.000	0.000	0.365	0.914	**0.006**	0.212	0.772	0.513	0.514	0.766
	N	165	165	165	165	165	**165**	165	165	165	165	165
Right motor cortex connectiviy	R	.246**	.332**	.354**	0.003	0.055	-0.112	0.143	-0.058	**.198***	-0.040	-0.011
	Sig.	0.001	0.000	0.000	0.968	0.481	0.151	0.067	0.459	**0.011**	0.613	0.888
	N	165	165	165	165	165	165	165	165	**165**	165	165
VMPFC connectivity	R	-.159*	.297**	-0.002	0.037	0.020	-0.012	-0.047	0.064	0.017	0.021	-0.024
	Sig.	0.041	0.000	0.983	0.637	0.802	0.874	0.552	0.418	0.831	0.784	0.759
	N	165	165	165	165	165	165	165	165	165	165	165
mSPL connectivity	R	0.099	.348**	.181*	-0.032	0.065	-0.001	0.024	0.004	0.099	-0.015	-0.138
	Sig.	0.206	0.000	0.020	0.682	0.406	0.991	0.759	0.959	0.207	0.847	0.076
	N	165	165	165	165	165	165	165	165	165	165	165

ILG cortical thickness	R	.196*	-0.006	0.067	0.031	0.103	0.044	-0.116	-0.077	-0.032	**-.155***	-0.024
	Sig.	0.012	0.936	0.394	0.695	0.186	0.577	0.139	0.323	0.684	**0.046**	0.756
	N	165	165	165	165	165	165	165	165	165	**165**	165

Table S 3. Bivariate correlations between connectivity scores and measures of ASD traits and mean levels of thoughts. Correlations that were identified previously by brain based analyses are in red. These analyses identified a correlation between connectivity scores between the ILG and left motor cortex, identified as related to total AQ scores, as significantly correlated with thinking in words (negatively related to the modality component). They also identified a correlation between ILG-right motor cortex connectivity, and the difference between off-task thought in the 0-back and 1-back. Finally, they identified a negative relationship between cortical thickness in the ILG and the difference between modality in the 0-back and modality in the 1-back, so that a larger mean cortical thickness in this area was related to thinking in words more in the 0-back. Significant relationships between brain measures and thoughts are highlighted in bold.
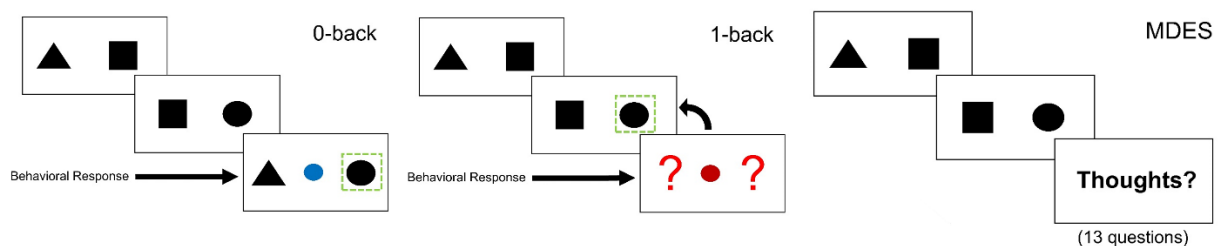
Figure S 1. Participants performed blocks of 0-back and 1-back tasks over three days. During the 0-back, on target trials, participants had to say which side of the screen the central blue shape was. During the 1-back, participants had to say which side of the screen the central red shape was on the previous trial. On a semi-random basis, the

target trial would be replaced by an MDES probe that asked the participant if their thoughts were focused on the task, followed by 12 questions about their thoughts.

A.4 Supplementary Materials: Chapter 6

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
Detailed	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

Table S1. Mind wandering questions asked to each participant during MDES. The first question was always "Task" then the other 12 questions in a random order. The scores from these questions were entered into a PCA.

Trial type	Relationship to time	Cluster size	p-value	MNI coordinates
Non-target	**Negative**	**33357** **359**	**<.0001** **<.0001**	**(12, -74, 34)** **(-30, 38, 32)**
Target	Negative	192	.0311	(4,46,-8)

Table S2. Description of the significant clusters produced by the contrasts of interest after correction at a cluster forming threshold of Z>3.1, p>.05 FWE-corrected.

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