Article:

Smallwood, Jonathan orcid.org/0000-0002-7298-2459, Turnbull, Adam, Wang, Hao ting et al. (16 more authors) (2021) The neural correlates of ongoing conscious thought. iScience. 102132. ISSN 2589-0042

https://doi.org/10.1016/j.isci.2021.102132 iScience

CellPress
OPEN ACCESS

Perspective

The neural correlates of ongoing conscious thought

Jonathan Smallwood,[1,10,*] Adam Turnbull,[1,12] Hao-ting Wang,[2] Nerissa S.P. Ho,[1] Giulia L. Poerio,[3] Theodoros Karapanagiotidis,[1] Delali Konu,[1] Brontë Mckeown,[1] Meichao Zhang,[1] Charlotte Murphy,[4] Deniz Vatansever,[5] Danilo Bzdok,[6] Mahiko Konishi,[7] Robert Leech,[8] Paul Seli,[8] Jonathan W. Schooler,[9,10] Boris Bernhardt,[6] Daniel S. Margulies,[11] and Elizabeth Jefferies[1]

SUMMARY

A core goal in cognitive neuroscience is identifying the physical substrates of the patterns of thought that occupy our daily lives. Contemporary views suggest that the landscape of ongoing experience is heterogeneous and can be influenced by features of both the person and the context. This perspective piece considers recent work that explicitly accounts for both the heterogeneity of the experience and context dependence of patterns of ongoing thought. These studies reveal that systems linked to attention and control are important for organizing experience in response to changing environmental demands. These studies also establish a role of the default mode network beyond task-negative or purely episodic content, for example, implicating it in the level of vivid detail in experience in both task contexts and in spontaneous self-generated experiential states. Together, this work demonstrates that the landscape of ongoing thought is reflected in the activity of multiple neural systems, and it is important to distinguish between processes contributing to how the experience unfolds from those linked to how these experiences are regulated.

Understanding the neural systems that support different patterns of thought is a long-term goal of cognitive neuroscience (Smallwood and Schooler, 2015; Christoff et al., 2016). However, the content of our thoughts and the form they take varies in a complex manner across people, places, and time (Figure 1). Since humans have the capacity for introspection, it is possible to use the technique of self-report to gain insight into the heterogeneous structure of these different patterns of experience. This approach is referred to as the experience sampling (ES) method (Hurlburt and Heavy, 2006; Hektner et al., 2007). Over the last decade, ES has become increasingly influential in the fields of psychology and cognitive neuroscience. This perspective piece considers recent work examining the neural correlates of ongoing experience, which account for both the content of ongoing thought and the way in which thoughts change depending on the situation we are in. These studies provide important evidence for the subtle context-dependent nature of the correlation between neural function and cognition and highlight that some neural systems, such as the default mode network (DMN), play a much more general role in cognition than has been hitherto anticipated.

Before continuing this review, it is important to recognize that self-reports can be an unreliable way to characterize cognition, as they are subject to contextual and motivational biases that the participants may themselves not recognize (Nisbett and Wilson, 1977). Problems with the validity and reliability of self-reports limit the potential for ES data to be useful as a tool for understanding cognition, and these inaccuracies can be quantified through a process of "triangulation"—an examination of the reliability of the correlations with replicable objective measures (Schooler, 2002). Box 1 considers the challenges that introspection poses in understanding ongoing thought patterns and how advances in neuroimaging and advanced statistical methods provide a number of strategies that can be helpful.

CONTENT, FORM, AND SITUATION AS BOUNDARY CONDITIONS IN UNDERSTANDING THE NEURAL CORRELATES OF ONGOING EXPERIENCE

Ongoing thought patterns can vary substantially across person, place, and situation (see top panel of Figure 1). Consequently, this section of this review considers how understanding the neural correlates of different thought patterns can be improved by (i) measuring multiple features of experience and (ii) including a range of different situations.

[1]Department of Psychology / York Imaging Centre, University of York, York, England

[2]University of Sussex, Brighton, England

[3]Department of Psychology, University of Essex, Colchester, England

[4]Department of Psychology, Cardiff University, Cardiff, Wales

[5]Fudan University, Shanghai, China

[6]Montreal Neurological Institute, McGill University, Montreal, Canada

[7]Laboratoire de Sciences Cognitives et de Psycholinguistique, Department d'Etudes Cognitives, ENS, PSL University, EHESS, CNRS, Paris, France

[8]Kings College, London, England

[9]Department of Psychology, duke University, Durham, NC, USA

[10]Department of Psychological and Brain Sciences, University of California, Santa Barbara, CA, USA

[11]Centre Nationale de la Researche Scientifique, Institute du Cerveau et de la Moelle epiniere, Paris, France

[12]University of Rochester School of Nursing, Rochester, NY, USA

*Correspondence: smallwoodjm@gmail.com

https://doi.org/10.1016/j.isci.2021.102132

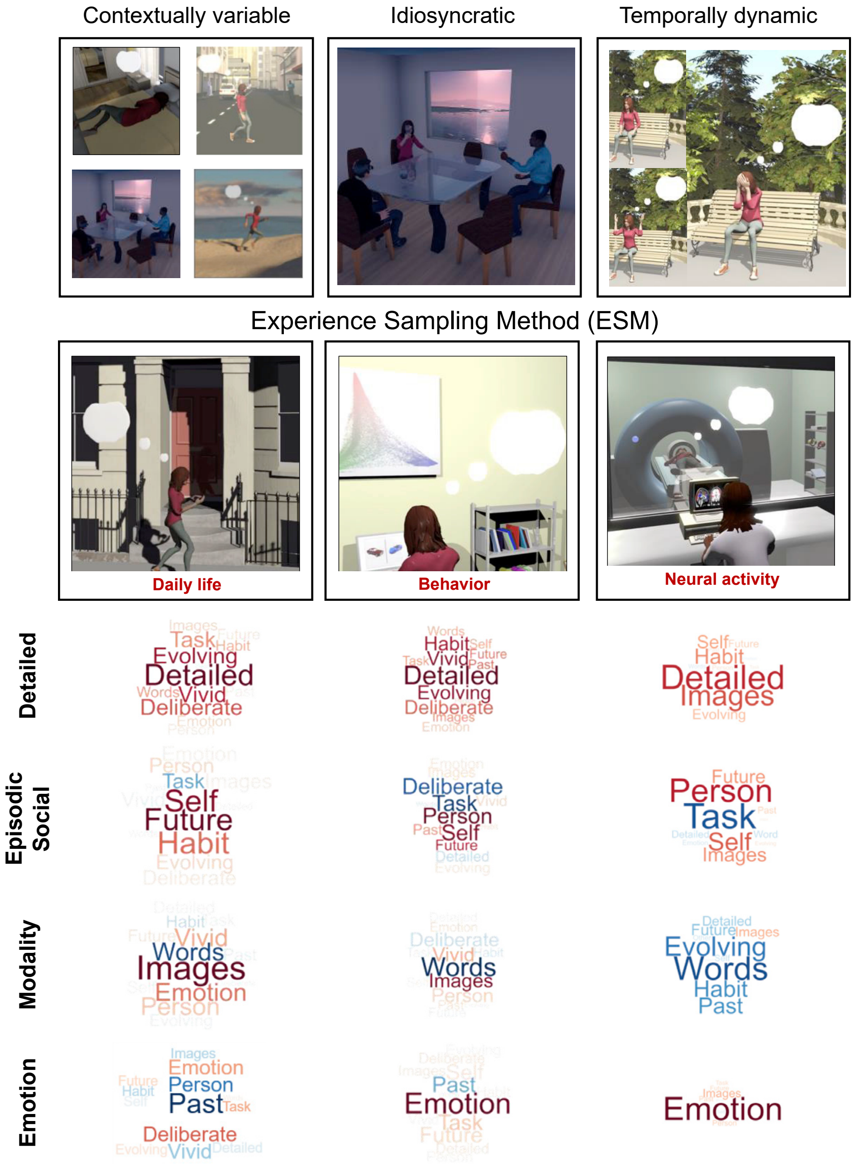

Figure 1. Heterogeneity in the patterns of ongoing thought

Upper panel. Using experience sampling to understanding patterns of experience. Ongoing experience varies across people, places, and time. Studies use experience sampling to gain better insight into the patterns of experience that are common in different individuals and in different situations, including in daily life. These can be related to objective behavioral and neural signatures recorded under laboratory conditions to help understand the neural contributions to different patterns of ongoing thought. Lower panel. Consistency in the latent structure of thought patterns as revealed through the decomposition of multi-dimensional experience sampling (MDES) data. The left-hand panel shows the results of the application of the same decomposition algorithm (principal components analysis, PCA) to sets of experience sampling questions recorded in different situations. It can be seen that this approach reveals a similar structure in reports across situations and that this structure is correlated across individuals. In this figure, the word clouds show the importance of the item through the font size (bigger = more important) and the direction of the association through the color (warmer colors = positive, cooler colors = negative).

Measuring the content and form of experience

Initial work linking ongoing experience to patterns of neural activity focused on specific states (e.g. off-task thought) (Smallwood et al., 2008; Christoff et al., 2009; Allen et al., 2013; Trautwein et al., 2016; Ellamil et al., 2016). By focusing on the neural correlates of experiential states, these studies have been useful in delineating the capacity to link patterns of reports to associated brain activity. However, by focusing on only a

Box 1. Using neuroimaging in combination with experience sampling to overcome the limitations of introspection as a tool for probing experience

There are a number of ways that advances in neuroimaging can help resolve issues linked to the problems of introspection as a scientific tool.

- Triangulation between neural function and both state and trait measures of experience.

Experience sampling can be used to chart momentary differences in the focus of attention by intermittently probing individuals under different experimental conditions to determine patterns of momentary experience (Csikszentmihalyi and Larson, 2014). However, patterns of experience can also be understood through their variation across a population as a dispositional trait (Fleeson and Gallagher, 2009). The possibility that spontaneous patterns can have trait-like features means that aspects of neural activity at rest are likely to be related to features of an individuals' cognitive or affective profile (Harmelech and Malach, 2013). When both trait- and state-like features of ongoing experience are combined with neural measures, the appropriate design can allow the evaluation of whether they both produce compatible conclusions. Figure 5 illustrates the results of such an approach. In one study (Turnbull et al., 2019b), measures of functional organization of neural function at rest were recorded in a large cohort of individuals. On subsequent days, the participants' patterns of ongoing thought were recorded in the laboratory. Since neural function was recorded before experience sampling occurred, dispositional associations between experience sampling and neural activity should be minimally impacted by experience sampling (Turnbull et al., 2019b). In a second study, neural activity was recorded at the same time that patterns of experience were recorded by self-report (Turnbull et al., 2019a). Measuring experience at the same time as neural function is likely to be more accurate in identifying the neural correlates of momentary experience, yet more likely to be biased by the act of introspection because both neural activity and self-report measures are acquired simultaneously. Both studies (Turnbull et al., 2019a; Turnbull et al., 2019b) highlighted regions of the ventral attention network (VAN) as important in the process of regulating attention in line with the demands of the task. The convergence between the conclusion of a dispositional and momentary analysis increases our confidence in the claim that the VAN plays an important role in contextual regulation of ongoing thought.

- Objective indicators of ongoing thought patterns

In multiple areas of neuroscience, advanced machine learning techniques have been used to understand the relationship between activity and function (Poldrack, 2008; Bzdok and Meyer-Lindenberg, 2018). Machine learning methods have been used to infer neural patterns associated with the performance of different tasks (Cole et al., 2013) and to discriminate features of perceptual content (Haxby et al., 2001; Kamitani and Tong, 2005). They have also been used to show that attentional states fluctuate over time (Rosenberg et al., 2020). Machine learning approaches could be leveraged to determine the occurrence of hidden thought patterns in a manner that is fully independent of self-report. It has already been shown that perceptual states can be decoded from neural patterns in the visual cortex (Miyawaki et al., 2008), and dream content can be decoded using the neural patterns that occur when participants are awake and view content with similar semantic features (Horikawa et al., 2013). Along similar lines (Tusche et al., 2014), used machine learning to discriminate task-induced examples of autobiographical memories with positive and negative features and demonstrated that these patterns can discriminate between spontaneously occurring examples of similar states. It is possible that these approaches could be fruitfully combined with approaches that use techniques like hidden Markov modeling or other ways of clustering data from fMRI (Karapanagiotidis et al., 2019; Vidaurre et al., 2017) or electroencephalograms (Pascual-Marqui et al., 1995; Michel and Koenig, 2018; Jin et al., 2019) to identify naturally occurring states. As our knowledge of the different patterns of ongoing thought and their associated neural correlates develops, pattern learning approaches are likely to become an increasingly useful tool in measuring covert states in an objective manner.

small number of dimensions of experience as these studies did, the mapping between observed patterns of neural activity and specific features of cognition can be ambiguous. For example, studies suggest that off-task thoughts often have more personally relevant episodic content than do on-task states (Baird et al., 2011; Huijser et al., 2018; Stawarczyk et al., 2011) especially when measured in the laboratory (Ho et al., 2020). Off-task states can also vary across individuals with respect to the degree to which they are deliberate (Seli et al., 2015), as well as in their focus on the future or the past (Smallwood et al., 2009). Other studies have shown that specific features of experience are most closely associated with task performance (van Vugt and Broers, 2016) and physiological measures such as pupillometry (Huijser et al., 2018; Konishi et al., 2017). Dimensions of experience are also often correlated, for example, with "intentional" thoughts described as more future focused (Seli et al., 2017). At the same time, features of experience that are assumed to be important, such as a sense of experiential dynamism, can be present in apparently opposing states (i.e. both task focused and task free) (Mills et al., 2018).

Similar covariation between domains is seen in neural studies—for example, there is similarity in the patterns of neural activity associated with experiences that are unrelated to the ongoing task and those referencing stimulus-independent features of mental content (Stawarczyk et al., 2011). Likewise, Christoff and colleagues (Christoff et al., 2009) found that regions showed a pattern of increased activity with off-task content that were often stronger when participants showed a relative absence of awareness of the contents of experience (often termed "meta-awareness") (Schooler, 2002). Finally, Kuyci and colleagues demonstrated that numerous brain regions, including those within the DMN, were related to patterns of off-task thought but that these relationships were more consistently seen when behavior was highly stable (Kucyi et al., 2016).

There is an emerging trend for researchers to explicitly address the covariation between multiple features, or dimensions, of experience by recording several features of experience at the same time (e.g. (Stawarczyk et al., 2013; Andrews-Hanna et al., 2013)). Once ES data have been recorded, techniques like principal component analysis or cluster analysis can be used to provide compact low-dimensional representations of the self-reported data. These low-dimensional representations can be loosely considered to describe "pattern of thoughts" that the participants reported during the study and can be represented as word clouds, where the polarity of the loading is indicated by the ink color and the magnitude is indicated by the font size (bigger = more important). Figure 1 shows an example of dimensions calculated in this way from data recorded in three different situations: in the behavioral lab, during neuroimaging and in daily life. It can be seen that dimensions produced in this manner produce word clouds with broadly similar features, and studies have shown that they have robust correlations across time (Konu et al., 2020).

Measuring experience across situations

Simple brain-experience correlations within only a single task context may make it difficult to distinguish features that are specific to the measurement context, from those that play a more general role in experience. For example, while elements of the DMN have been linked to being "off-task" in sustained attention (Trautwein et al., 2016) and aversive situations linked to nociception (Kucyi et al., 2013), features of the default mode are also important for tasks such as reading (Mar, 2011). Accordingly, neural links with ongoing experience during reading are complex. For example, studies have shown that regions of the DMN, such as the posterior cingulate cortex or the lateral temporal cortex, contribute to both better and worse focus on the task during reading, depending on their pattern of connectivity with other neural regions (Zhang et al., 2019; Smallwood et al., 2013). If neural systems contributing to different types of thought patterns vary as a function of the task context, it will be likely that the functional implications of brain-cognition relationships will be mischaracterized if they are only sampled in a single task context.

Contemporary research, therefore, converges on the assumption that in order to fully characterize the role specific neural substrates plays in ongoing experience, it is necessary to sample more than one task environment. More generally, this observation has importance for the generalizability of accounts of neural function. For example, we found that individual variation in patterns of emotional thoughts shows the least generalizability between the laboratory and daily life and that both patterns of detailed and off-task thought are correlated across individuals and can show similarities in their relationship to gray matter architecture (Ho et al., 2020).

Summary

Understanding the neural correlates of different patterns of thought requires both (1) the measurement of multiple aspects of ongoing experience at the same time to control for complex relationships between different experiential features and (2) the assessment of experiences across a range of situations in order to isolate contextual influences from more general influences. With these issues in mind, we next consider recent studies exploring the neural basis of the experiential features of different thought patterns that use designs that involve these methodological features.

MAPPING THE NEURAL FEATURES OF DIFFERENT ONGOING THOUGHT PATTERNS

When participants perform a wide range of difficult external tasks, they increase activity in a common set of distributed regions anchored in lateral parietal and frontal regions, which are often referred to as the task-positive or multiple demand network (MDN) (Duncan, 2010). In the lower panel of Figure 2, these "task-positive" systems are represented in dark blue. In contrast, neural activity in a different set of regions decreases when tasks get harder but often remains active in the absence of a task. This network includes a set of regions anchored by the posterior cingulate and medial prefrontal cortex and is known as the DMN (Raichle

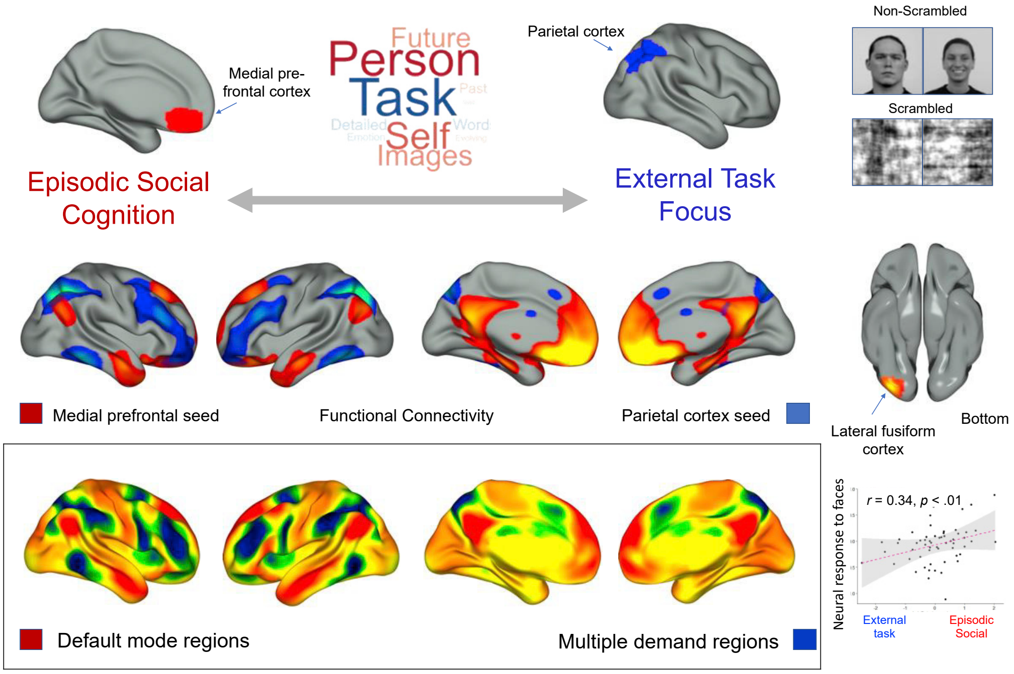

Figure 2. Neural regions dissociating external task focus and states of episodic social cognition reflect opposing ends of a task-positive hierarchy

Studies highlight that regions which are active during external task focus (shown in blue) and during self-generated episodic social thought (shown in red) fall at opposing sides of a neural hierarchy that describes the brain response to external tasks. The top left panel shows greater neural activity within the ventral medial prefrontal cortex when individuals engage in social episodic thought (Konu et al., 2020). The top right panel shows regions of the intra-parietal sulcus exhibiting greater activation when individuals are engaged in external task focus (Turnbull et al., 2019a). The word clouds describe the experience patterns associated with each pattern of neural response. The middle and lower panel shows the functional connectivity of these two regions (colored appropriately), and it can be seen that the distribution of these maps parallel a dimension in connectivity space which describes the brain response to increasing task demands from the study by (Margulies et al., 2016). The right-hand subpanel shows a region of the lateral fusiform cortex that shows greater activity when viewing faces for individuals who spent more time engaged in off-task thought in a separate laboratory session.

et al., 2001). The regions of the DMN are indicated in the lower panel of Figure 2 in red. Initial interpretations of the deactivation observed in the DMN focused on the possibility that it supports task-negative functions, e.g (Fox et al., 2005). However, more recent studies suggest that this system is important in certain active mental processes, particularly those linked to memory or social processes. Endel Tulving (Tulving, 2002) coined the term "mental time travel" to describe the type of thinking that participants engage when they imagine the future or recall the past. Studies have confirmed a role for regions within the DMN in aspects of mental time travel (e.g. [Spreng et al., 2009]), as well in tasks tapping both semantic (Binder et al., 2009; Vatansever et al., 2017) and episodic memory (Sestieri et al., 2011). More broadly, regions in the DMN are important when information in memory can guide external task decisions (Konishi et al., 2015; Murphy et al., 2018, 2019a; Vatansever et al., 2017). Importantly, applications of advanced machine learning to resting-state functional connectivity have demonstrated that the DMN and MDN form two extremes of a neural hierarchy that is commonly assumed to represent how the brain responds to tasks which vary on their cognitive demands (Margulies et al., 2016). Generally, the MDN regions tend to increase when tasks are difficult, while the regions of the DMN often show the opposite pattern of behavior (i.e. reducing its level of activity).

Beyond perception-action: the neural correlates of self-generated states

Contemporary accounts of ongoing thought argue that attention toggles between modes of perceptually guided and self-generated thoughts over time (Smallwood, 2013). Consistent with this observation, studies highlight a pattern of experience which is anchored at one extreme by a state of deliberate task focus and at the other by patterns of episodic social cognition (see the second column in Figure 2 and center of main

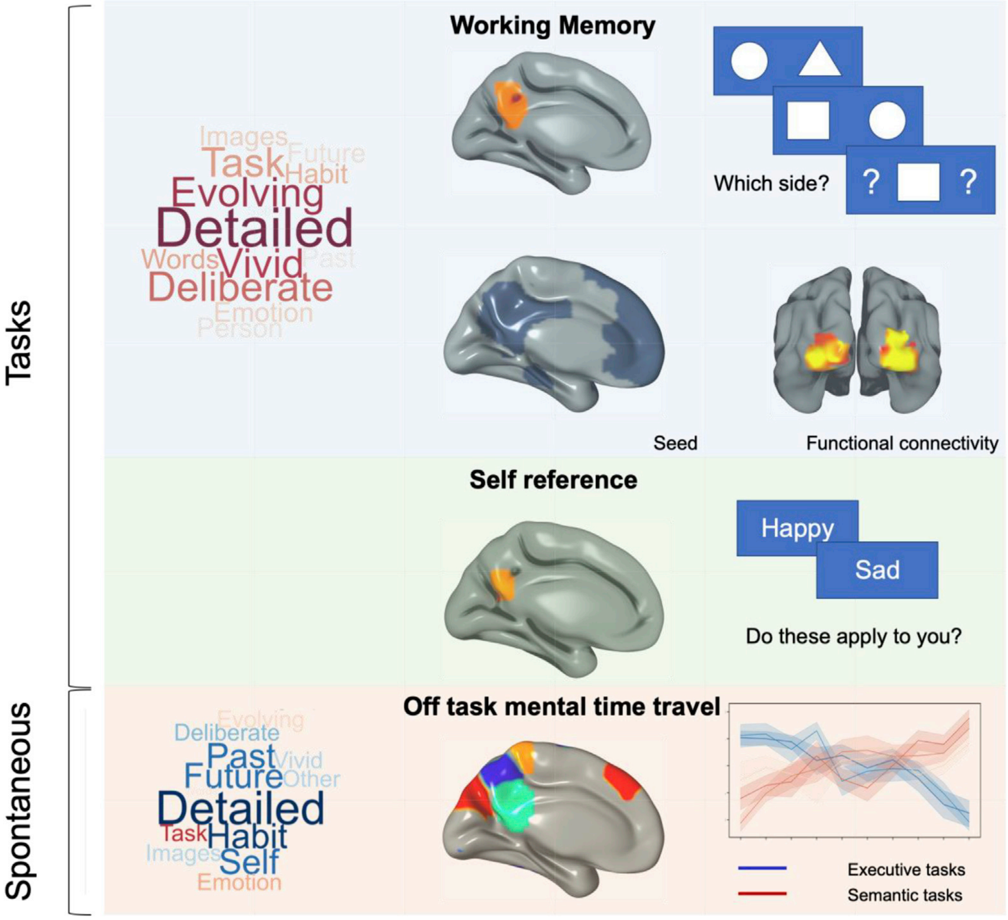

Figure 3. Regions of the posterior cingulate cortex are implicated in reports of vivid detailed thought across a range of states

The top panel (colored blue) shows evidence of the role of the DMN, and in particular a region of posterior cingulate, in detailed task-relevant cognition during working memory. In a study measuring neural activity in conjunction with subjective reports of ongoing thought patterns, a region of the posterior cingulate cortex was identified that exhibited a stronger positive association with reports of detailed task-relevant experience during working memory than in a less demanding task variant (Turnbull et al., 2019b). In an individual difference study in which participants performed a similar paradigm in the laboratory and brain activity was recorded at rest, individuals who reported high levels of external detail during task performance in the lab exhibited greater functional connectivity between the default mode network and regions of the visual cortex (Turnbull et al., 2019b). The middle panel (colored green) shows greater activity in regions of the posterior cingulate cortex during self-reference for participants who maintained high levels of detail in a separate laboratory session (Murphy et al., 2019b). The lower panel (colored red) shows the results of a canonical correlation analysis highlighting neural regions, including the posterior cingulate cortex, as linked to both expertise in semantic processing and patterns of ongoing thought characterized by vivid mental time travel. Note the different associations between the term "task" and "detail" in the upper and lower word clouds in this figure, which imply that these states share high levels of detail but differ with respect to whether they refer to detailed task-relevant cognition or detailed self-generated thought.

panel Figure 3). Figure 2 shows that this pattern is broadly reproducible in studies in the lab and daily life (Ho et al., 2020) and when the same task is performed in the scanner and in the laboratory (Sormaz et al., 2018).

A series of studies explicitly explored neural activity associated with this dimension of experience (Konu et al., 2020; Turnbull et al., 2019a). In one study, recruitment of neural activity in regions of the lateral parietal cortex was observed when participants' reports indicate a deliberate focus on task-relevant material (in blue, see right top brain Figure 2). Importantly, this pattern was equivalent in both an easy and a more demanding task context (Turnbull et al., 2019a), suggesting that these dorsolateral parietal regions are important in maintaining external task-relevant information regardless of the difficulty of the task. In contrast, when participants' experience is dominated by episodic social features, increased neural recruitment is observed in regions of the ventral medial prefrontal cortex ((Konu et al., 2020) in red, see the left top brain, Figure 3). Prior research has confirmed activity in this cortical region during ''off-task'' states (Christoff et al., 2009; Allen et al., 2013; Trautwein et al., 2016; Stawarczyk et al., 2011).

It is clear from Figure 2 that in the context of sustained attention, task-related features of ongoing thought are related to the parietal cortex, while the self-generated episodic content is related to regions in the DMN, in this case ventromedial prefrontal cortex (vMPFC). The middle panel of Figure 2 shows the resting-state functional connectivity of the regions showing associations between states of task focus (blue) and episodic social cognition (red) from the relevant studies. It can be seen that these maps are largely non-overlapping and correspond to the two extremes of the task-positive hierarchy as characterized by a prior study (Margulies et al., 2016). Together, therefore, these studies establish a correspondence between a dimension identified through ES, reflecting trade-offs between internal and external domains, and a neural hierarchy that describes the brain's response to increasing task demands.

In order to confirm the psychological features of ''social episodic'' cognition, Ho and colleagues (Ho et al., 2020) conducted an individual difference experiment that examined how variation in episodic and social aspects of thought is related to neural responses to stimuli with real-world significance (faces and scenes) measured using functional Magnetic Resonance Imaging (fMRI). They found that individuals who tend to prioritize patterns of social episodic cognition under laboratory conditions show greater activation in a region of lateral fusiform associated with face perception when viewing faces. This result is presented in the right panel of Figure 3 and provides confirmatory evidence that individuals prone to off-task thought show heightened neural sensitivity to person-relevant stimuli. Since the term ''person'' is dominant in this pattern of thought (see word cloud), this result provides converging neural and experiential support for the view that the off-task state can have important social features (Schilbach et al., 2008).

Immersive experience—a role for the DMN in more detailed patterns of ongoing thought

As well as representing different types of experiential content (for example, task-relevant or episodic-social content), patterns of ongoing thought can also vary with respect to how immersive they feel. Analyses of the contents of ongoing thought provided by multi-dimensional experience sampling (MDES) show evidence of a pattern of immersive detailed thinking that is linked to task-relevant processing in both the real world and in the lab (Ho et al., 2020) (see top row in Figure 1). In the laboratory, this pattern is most prominent in executively demanding tasks (Turnbull et al., 2019b).

Studies have linked states of detailed task-relevant ongoing thought to neural activity in the DMN. For example, when participants perform tasks requiring the maintenance of spatial information in working memory, neural signals in this region contain information regarding patterns of detail thought during working memory maintenance (Sormaz et al., 2018). Moreover, whole brain analyses localized this pattern to the posterior cingulate cortex where greater neural activity is linked to task-relevant thoughts with greater detail in a 1-back working memory context (Turnbull et al., 2019a) (see top panel Figure 3). An individual difference analysis established that individuals who have more detailed task-relevant thoughts in the lab show greater correlation between the DMN and regions of the lateral visual cortex at rest (Turnbull et al., 2019b). This suggests that patterns of detailed experience partly depend on co-ordination between the DMN and visual cortex. Together, these data suggest that neural processes in the DMN, especially posterior regions, can be associated with more detail task-relevant thought. This pattern may be the subjective correlate of the observation that nodes within the DMN become more integrated with systems involved more directly in perception and action during more challenging working memory tasks (Vatansever et al., 2015). It may also be linked to the observation that the DMN can play a role in being ''in the zone'' during task performance (Kucyi et al., 2016). It is worth noting that collectively these lines of evidence are inconsistent with a role of the DMN as purely task-negative or relevant to purely autobiographical content.

In order to fully understand the associations between detailed experience and neural signals within the DMN, it is important to establish whether a similar relationship extends beyond the context of cognitively demanding working memory tasks. Prior task-based studies have shown that precise and vivid features of episodic memory are linked to regions of the default mode including both the angular gyrus and precuneus

(Richter et al., 2016; Bonnici et al., 2016). Similarly, disruption of the angular gyrus via transcranial magnetic stimulation selectively impairs specific features of semantic retrieval (Davey et al., 2015). Building on these relationships, Murphy and colleagues (Murphy et al., 2019b) examined neural activity during the act of self-reference in a group of individuals for whom we had pre-established their tendency to report different aspects of experience during sustained attention tasks within the laboratory. This study found that individuals who report patterns of detailed task-relevant thoughts in the lab exhibited greater recruitment of the posterior medial cortex during the act of self-reference (see middle panel in Figure 3).

Finally, it is important to determine whether there is any role for the DMN and patterns in detailed thoughts that are only loosely related to ongoing external tasks. To address this goal, Wang and colleagues used an advanced machine learning technique known as canonical correlation analysis (CCA, for a review see [Wang et al., 2018a]). CCA allows the simultaneous decomposition of data sets with different features, in this case performance trade-offs across a battery of cognitive tasks and patterns of individual variation in the functional architecture of individuals at rest. They found that a pattern associated with better semantic performance (picture naming and category fluency) relative to executive control tasks (switching and digit span) was linked to a distributed pattern of connectivity that encompassed the posterior cingulate (Wang et al., 2019)—a pattern consistent with a role of semantic processing in imagination (Irish, 2019). In a separate laboratory session, these individuals reported a pattern of self-generated mental time travel in the laboratory characterized by higher levels of detail. It can be seen in the word cloud in the lower panel of Figure 3 that the term ''detailed'' is associated with less task-relevant processing (the word ''task'' is colored blue), whereas the terms ''detailed'' and ''task'' both have similar loadings in the upper word cloud (and also in daily life see Figure 1). This indicates that the two patterns of experience both have detailed features, and both are linked to the posterior cingulate, yet are differentiated in terms of whether they are task relevant or not. Viewed together, these data suggest a role for the posterior cingulate in detailed cognition that encompasses both internal and externally directed experiential states.

It is also possible that connections between the hippocampus and the posterior cingulate are important for the processes that give rise to detailed experiences. A seed-based functional connectivity study found that individuals with greater connectivity between the hippocampus and the posterior cingulate reported patterns of more detailed thoughts in the laboratory (Smallwood et al., 2016). Furthermore, in an independent set of participants, greater cortical thickness in the anterior para hippocampus was linked to patterns of evolving detailed task focus in the laboratory and in daily life (Ho et al., 2019, 2020), supporting prior studies which show a role of the hippocampus in evolving thoughts (Ellamil et al., 2016). In healthy controls, increased connectivity between the medial temporal lobe and posterior cingulate is linked to more extreme mind wandering, while this relationship is not observed in either frontotemporal dementia or Alzheimer disease (O'Callaghan et al., 2019). Finally, in Alzheimer disease, dysregulation of the posterior cingulate cortex is linked to a lack of details in episodic thoughts (Irish et al., 2015).

Together, these studies establish a role for regions of the DMN in patterns of detailed, evolving ongoing thought across a broad range of contexts, including complex tasks such as working memory, and spontaneous self-generated states. This suggests a role of the DMN that extends beyond either a simple task negative or a traditionally episodic view of this system's functional contribution to cognition. Collectively, our data suggest that the DMN, or at least the posterior cingulate cortex (pCC), makes a broad contribution to ongoing experience that is generally related to how detailed, or, immersive experiences are (Leech and Smallwood, 2019). One hypothesis is that this role is made possible because the DMN is located at the apex of a cognitive hierarchy in humans, allowing it be involved in multiple different modes of operation (Margulies et al., 2016). Moreover, the apparent role of the DMN in highly detailed experiences suggests it may help establish a sense of ''presence'' which is the subjective experience of being in one place or environment and that is assumed to be important in states of immersion in virtual environments (Witmer and Singer, 1998). Consistent with this possibility, studies suggest that neural processes in regions of the posterior cingulate cortex and hippocampus are important in our sense of where we are and of body ownership in virtual environments (Guterstam et al., 2015)

THE MAINTENANCE AND DYNAMICS OF ONGOING THOUGHT PATTERNS OVER TIME

One important feature of patterns of ongoing thought is that they are dynamic (Christoff et al., 2016; Smallwood, 2013). As well as understanding how we are able to represent information relevant to both perceptually guided and self-generated thought patterns, it is important to understand the neural correlates of how we maintain these patterns over time, as well as to be able to flexibly switch between these states in an appropriate manner.

Regulating ongoing thought patterns in line with environmental demands

Studies suggest that the ability to stay on task during complex tasks is linked to better performance (Smallwood et al., 2008) and that this may be mediated via executive control (McVay et al., 2009; McVay and Kane, 2012; Unsworth and McMillan, 2014). On the other hand, studies have suggested that dispositional variation toward engaging in self-generated thought (such as daydreaming) is associated with tasks linked to better creativity and problem solving (Zedelius and Schooler, 2015; Gable et al., 2019; Wang et al., 2018b; Leszczynski et al., 2017). Likewise, periods of self-generated thinking are hypothesized to provide opportunities for making personal goals concrete (Stawarczyk et al., 2011; Medea et al., 2018; Niedźwieńska and Kvavilashvili, 2018). Consequently, since there may be benefits to both and internal and external focus, it has been proposed that adaptive cognition requires the ability to regulate patterns of thought to ensure that they are appropriate to the demands imposed by the external environment. This view is known as the "context regulation hypothesis" (Smallwood and Andrews-Hanna, 2013).

To test the context regulation hypothesis, Turnbull and colleagues (Turnbull et al., 2019a) measured neural activity while participants performed a task which alternated between blocks of low and high demands through the manipulation of working memory load. Under these conditions, individuals generally maintain task focus during the harder blocks and engage in greater off-task episodic thought during the easier blocks (Smallwood et al., 2009; Teasdale et al., 1993). This difference is usually more pronounced for individuals who tend to perform well on cognitive measures that are thought to be associated with better control (Turnbull et al., 2019b; Rummel and Boywitt, 2014; Levinson et al., 2012; Smallwood et al., 2013).

Turnbull and colleagues found that neural activity in a region of the left dorsolateral prefrontal cortex (dLFPC) shows a pattern of greater neural activity when participants engaged in task focus during demanding external tasks and during greater off-task social episodic thought while individuals performed the easier task blocks (see Figure 4). This region is within the ventral attention network (VAN), as defined by Yeo and colleagues (Yeo et al., 2011), and meta-analysis of its functions highlighted processes linked to "executive control" (Turnbull et al., 2019a). Notably, lesions in this region are linked to problems regulating both internal and external cognition (Kam et al., 2018). Moreover, Turnbull and colleagues found that, at rest, the VAN shows greater correlation with a region of the left motor cortex for individuals who showed a better ability to regulate their thoughts to ensure that they are compatible with environmental goals (i.e. who reported more on-task thought in more demanding tasks and more off-task thought when the task was easier) (Turnbull et al., 2019b). Together, these studies highlight a role for the VAN as important for prioritizing patterns of ongoing thoughts that transcend a specific focus of attention (because this network was associated with both external and internal focus). Instead, this evidence is consistent with a role of this system in the alignment between a person's broader goals and the demands of the environment and thus may be important for stabilizing salient cognitive states (Dosenbach et al., 2007). Furthermore, the study highlights interactions between this system and regions linked to motor behavior as one mechanism through which better context regulation is achieved. Consistent with this possibility, individuals describe off-task thoughts as more intentional during easy tasks (Seli et al., 2016), and more intentional off-task thoughts are associated with greater functional connectivity with a similar region of the motor cortex (shown in the lower right hand panel, Figure 4 [Golchert et al., 2017]).

Intrinsically motivated changes in ongoing experience

As well as changing in a manner determined by environmental demands, patterns of ongoing thought also vary naturally with the passage of time. The neural basis of these intrinsic changes can be explored using two complementary methods. One approach is to exploit the advanced machine learning method that allows time varying neural data to be decomposed into state-related patterns. Approaches such as hidden Markov modeling (HMM) and other dynamic approaches have been argued to be important for understanding dynamic state-like features of spontaneous thought (Kucyi, 2018; Zanesco, 2020). Karapanagiotidis and colleagues (Karapanagiotidis et al., 2019) applied HMM to resting-state data in a large cohort of participants for whom samples of experience had been recorded at the end of the scan. They found that states identified in this manner tend to fall toward the extreme end of one or more of the large-scale neural hierarchies. It can be seen in the top left panel of Figure 5 that the naturally occurring states (indicated by the colored dots) fall outside of the distribution generated through permutation testing (indicated by the

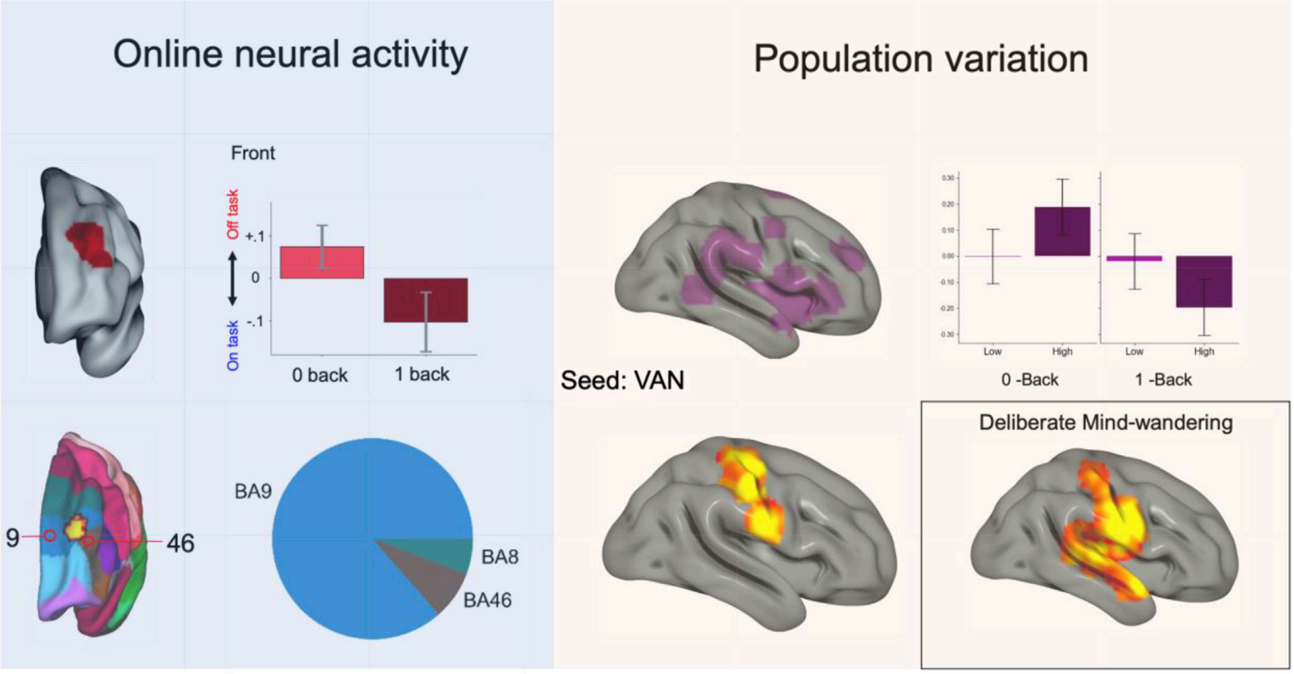

Figure 4. Studies have highlighted the role of the ventral attention network (VAN) and in particular region BA 9/46 in the dorsolateral prefrontal cortex as important in regulating patterns of ongoing thought to ensure that they are appropriate given the demands imposed by the external environment

The left panel shows the neural correlates of context regulation. Activity within a region of the left dorsolateral prefrontal cortex (shown in red) is associated with social-episodic thought when task demands are low and task focus when task demands are higher (Turnbull and et al., 2019a). The middle panel shows the functional architecture supporting better context regulation. Individuals who show better alignment of cognition with task demands in the laboratory show greater connectivity between the VAN (shown in purple) with a region of the left motor cortex (shown in yellow) at rest (Turnbull et al., 2019b). The lower right subpanel shows that a similar region of left motor cortex connectivity at rest is associated with greater levels of intentional mind wandering (Golchert et al., 2017) that maybe the hallmark of more contextually regulated ongoing thought (Seli et al., 2016).

gray contours in the plot). Notably, the time that participants spent in two states had reliable multivariate associations with the ES data collected at the end of the scan. These are presented in the middle top panel of Figure 5, showing both the neural organization of the states and the associations with experience in the form of word clouds. Psychologically, these states corresponded to "unpleasant intrusive" experiences as well as a pattern of "autobiographical planning". Notably, these two states occupied opposing ends of the neural hierarchy describing the brain's response to complex task demands, with states of planning resembling the patterns seen during complex task performance (see histogram in the top right panel).

A second method for understanding the dynamics of ongoing thought uses ES to characterize how cognition changes with respect to time. Turnbull and colleagues (Turnbull et al., 2020) examined the neural changes that emerged as time passes between moments of action during sustained attention tasks. ES was recorded concurrently with brain activity. They found that maps describing the regional impact of the passage of time were spatially correlated with the map describing the neural response to task demands (gradient 3, lower panel Figure 1). This indicates that as time passed, task-positive regions tended to decrease in activity while regions in the DMN tended to increase. A conceptually similar pattern was observed when comparing neural maps derived from ES studies which describe the difference between being on-task or thinking about self-generated social episodic information. It can be seen in the scatterplot in the lower left panel in Figure 5 that the spatial maps relating to time and attentional state occupy similar regions within the three-dimensional gradient space—regions increasing activity are located closer to the off-task state.

Summary

Studies examining dynamic properties of ongoing thought have revealed the influence of systems that help stabilize patterns of experience in line with the demands on cognition, as well as intrinsic influences that

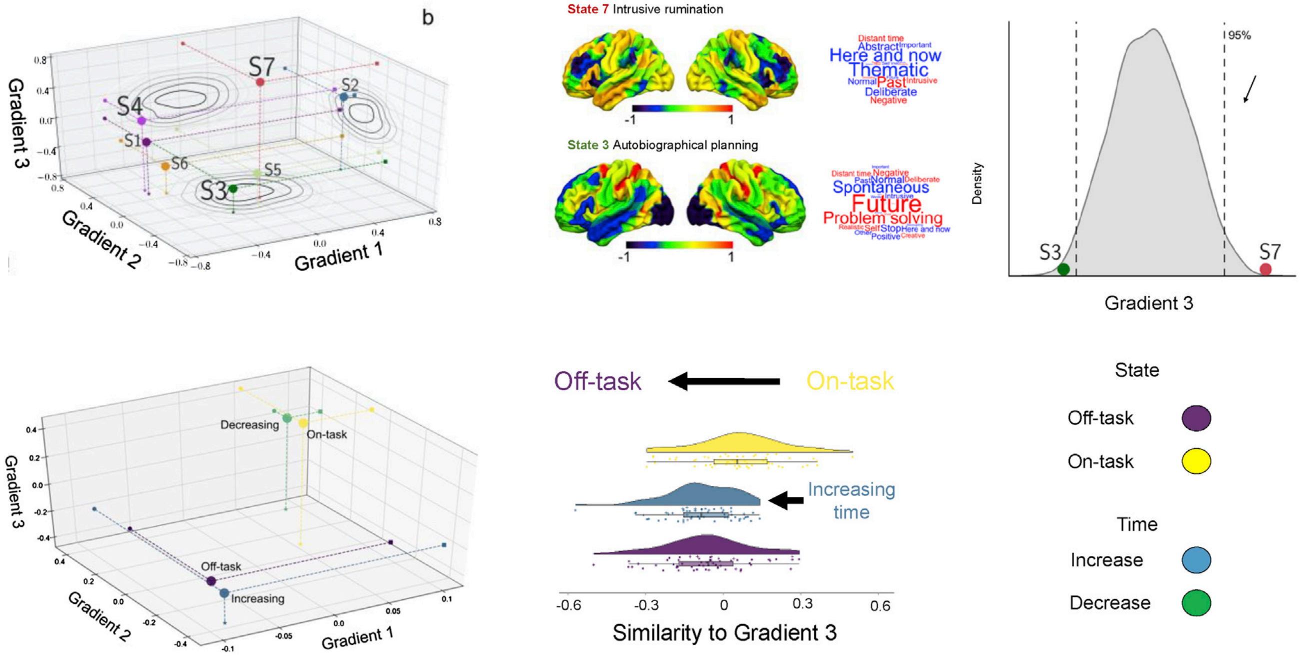

Figure 5. Dynamic features of ongoing experience reflect the role of task-related hierarchies as an organizing framework for differentiating patterns of thought

Analysis of the distribution of naturally occurring neural states at rest show that these hidden states tend to cluster toward the extreme ends of each of three well-described neural hierarchies (Gradient 1 unimodal-transmodal, Gradient 2 visual-motor, and Gradient 3 task-positive/task negative). Top left panel shows that states identified using hidden Markov modeling (HMM) tend to fall outside the region that corresponds to the distribution of synthetic states (indicated as contour plots and generated via permutation testing). The middle top panel shows the spatial motifs of two states identified that had multivariate associations with patterns of ongoing experience (displayed as word clouds). These broadly correspond to a state of unpleasant rumination and future planning. The histogram highlights that these states were differentiated along a connectivity gradient that resembles the effect of task demands on cognition (gradient 3). It is also possible to explore the dynamics of ongoing thought using experience sampling in a task. States of on-task thought tend to decline over time, and this phenomenon can be visualized by calculating the similarity in spatial maps that describe neural processes that changes with time during task performance and relating these to spatial maps which describe the difference between being on task or focused on social episodic states. These are presented in the lower middle panel of this figure. The lower right plot shows that both maps associated with being on task or engaged in social episodic thought occupy opposing sides of gradient 3. Neural estimations of regions that change the most with time occupy similar positions on the same dimension (regions that decrease the most are closer to the on-task state, while regions that increase the most with time are close to the social episodic patterns).

emerge with the passage of time. Importantly, these data highlight that it is likely to be an oversimplification to equate neural patterns linked to spontaneous thought as similar to neural motifs synonymous with easy or automatic situations since (a) the occurrence of patterns of neural organization normally seen during the performance of difficult tasks can also be linked to patterns of self-generated thoughts, albeit those with relatively task-like features (i.e. problem solving, deliberate, and future focused, see Figure 5), and (b) regions of the dLFPC can play a role in prioritizing both task-relevant information and self-generated experience (see Figure 4).

IMPLICATIONS AND FUTURE DIRECTIONS

The studies reviewed in this paper establish the complex role that neural processes play in patterns of ongoing thought. Critically, this review highlights the need for future studies to account for the heterogeneity of experiences using techniques such as MDES, which can capture multiple different features of experience. These rich data can be explored using data-driven methods to provide descriptions of different qualities of experience that provides a contrast to studies that focus on specific features of experience. For example, recent philosophical considerations of research on "mind wandering" suggest that there are epistemological problems with this construct as it is often operationalized (Irving and Glasser, 2020), and it is possible a data-driven taxonomy could be useful when addressing relationships between mental autonomy and conscious experience (Metzinger, 2018). Furthermore, it is essential that future studies must seek to assess the psychological and neural correlates of different types of experiences across a broader range of task contexts. This review has shown that without measuring different task contexts, associations between neural systems and ongoing thought patterns can easily be mischaracterized. As well as providing clear criteria for future experimental work focused on understanding the neural correlates of ongoing experience, these studies also have general implications for understanding the roles specific brain systems play in cognition.

Attention and control systems can play a broad role in the maintenance of goal states that extends beyond external tasks

Data considered in this review (see Figure 2) show that the dLFPC, a region embedded in the VAN, plays a role in the expression of thoughts that they have apparently opposing content: the dLPFC was associated with on-task thoughts when external task demands are higher and patterns of off-task social episodic thoughts when external task demands were lower. In contrast, regions of the intra-parietal sulcus (IPS), a member of the dorsal attention network (DAN), has a relationship with thought patterns that is more closely tied to the direction of attention. Activity in the IPS was linked to external task focus in both easier and harder tasks. Both the dLPFC cortex and IPS are members of the so-called MDN (Assem et al., 2020), and the contrasting associations these regions have with respect to ongoing thought patterns suggest a novel way to fractionate this network. It is possible that the dLPFC may play a more abstract role than the IPS since the former helps prioritize ongoing thought patterns regardless of whether they require an internal or external focus to attention. In contrast, the IPS is apparently more closely tied to interacting directly with the outside world since its activity was only linked to thoughts related to an external task. Accordingly, patterns of increased activity in the MDN observed during difficult external tasks may reflect two types of processes. Regions such as the IPS (and perhaps other regions of the DAN) may be engaged when attention is focused externally, while regions such as the dLPFC (and perhaps other regions in the VAN) may be engaged when thoughts need to be prioritized in line with the agent's current goal state. Notably, this fractionation of the MDN system is anticipated by recent formulations of the neural basis of spontaneous thoughts (Christoff et al., 2016).

Furthermore, the existence of regions with a dedicated role in the maintenance of external task-relevant input (e.g. IPS) raises the possibility that there may also be regions that exert a greater influence on internally represented content (e.g. memories). Regions including the posterior middle temporal gyrus and the inferior frontal gyrus (IFG) have been argued to be important in the selection of memories in line with task demands, forming a network important for the process of semantic control (Noonan et al., 2013). These regions may exert influence on internally represented information because they are closely aligned functionally to elements of the DMN than are other elements of the MDN (Noonan et al., 2013; Dixon et al., 2018). These data raise the possibility that certain aspects of the brain's executive control system may be relevant to influencing how memories contribute to ongoing thoughts. Important preliminary support for this idea comes from evidence that patterns of brain activity dominated by connections between the IFG and the angular gyrus are associated with reports that individuals spent their time at rest engaged thinking deliberate thoughts on a theme familiar to themselves (Vatansever et al., 2017). Future studies could extend our understanding of this possibility by examining whether regions important for controlled retrieval of information from memory as part of an externally motivated task are also important for the support of patterns of self-generated thought with more controlled features.

The default mode network role in ongoing thought goes beyond task-negative or strictly autobiographical processes

Although studies show that regions of the medial prefrontal cortex can play an important role content related to off-task states during sustained attention (Konu et al., 2020), they also show that the same system can contribute to task focus when reading (Zhang et al., 2019). The most direct evidence for the role of the DMN in both task-related and spontaneous aspects of ongoing thoughts is in the contribution of the pCC to highly detailed patterns of thought (Figure 5). In particular, our analysis suggests that the pCC plays a general role in ongoing thought patterns—contributing to experiences with higher levels of detail across different task contexts and in spontaneous states. Since this occurred across multiple different contexts, including complex external tasks, this pattern is inconsistent with views on the DMN as facilitating purely automatic (Shamloo and Helie, 2016), social (Jenkins, 2019), or self-relevant (van der Linden et al., 2020) processes. Instead, these results are consistent with the notion that certain regions of the DMN play a role in ongoing experience that is linked to ''how'' experiences emerge or unfold (Leech and Smallwood, 2019), possibly reflecting a role of the DMN in supporting more integrated forms of cognition (Mckeown et al., 2020). It will also be important to determine the extent to which different thought patterns recruit the

DMN as a whole or instead whether different mental states fractionate the "canonical" DMN, creating subnetworks that are engaged in different types of cognitive state.

ACKNOWLEDGMENTS

This research was supported by a European Research Council consolidator award to the first author (WANDERINGMINDS - 646927). E.J. was supported by a European Research Council consolidator award (FLEXSEM – 771863).

REFERENCES

Allen, M., Smallwood, J., Christensen, J., Gramm, D., Rasmussen, B., Jensen, C.G., Roepstorf, A., and Lutz, A. (2013). The balanced mind: the variability of task-unrelated thoughts predicts error-monitoring. Front. Hum. Neurosci. *7*, 743.

Andrews-Hanna, J.R., Kaiser, R.H., Turner, A.E., Reineberg, A.E., Godinez, D., Dimidjian, S., and Banich, M.T. (2013). A penny for your thoughts: dimensions of self-generated thought content and relationships with individual differences in emotional wellbeing. Front. Psychol. *4*, 900.

Assem, M., Glasser, M.F., Van Essen, D.C., and Duncan, J. (2020). A domain-general cognitive core defined in multimodally parcellated human cortex. Cereb. Cortex *30*, 4361–4380, https://doi.org/10.1093/cercor/bhaa023.

Baird, B., Smallwood, J., and Schooler, J.W. (2011). Back to the future: autobiographical planning and the functionality of mind-wandering. Conscious Cogn. *20*, 1604–1611.

Binder, J.R., Desai, R.H., Graves, W.W., and Conant, L.L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. Cereb. Cortex *19*, 2767–2796.

Bonnici, H.M., Richter, F.R., Yazar, Y., and Simons, J.S. (2016). Multimodal feature integration in the angular gyrus during episodic and semantic retrieval. J. Neurosci. *36*, 5462–5471.

Bzdok, D., and Meyer-Lindenberg, A. (2018). Machine learning for precision psychiatry: opportunities and challenges. Biol. Psychiatry Cogn. Neurosci. Neuroimaging *3*, 223–230.

Christoff, K., Gordon, A.M., Smallwood, J., Smith, R., and Schooler, J.W. (2009). Experience sampling during fMRI reveals default network and executive system contributions to mind wandering. Proc. Natl. Acad. Sci. U S A *106*, 8719–8724.

Christoff, K., Irving, Z.C., Fox, K.C., Spreng, R.N., and Andrews-Hanna, J.R. (2016). Mind-wandering as spontaneous thought: a dynamic framework. Nat. Rev. Neurosci. *17*, 718.

Cole, M.W., Reynolds, J.R., Power, J.D., Repovs, G., Anticevic, A., and Braver, T.S. (2013). Multi-task connectivity reveals flexible hubs for adaptive task control. Nat. Neurosci. *16*, 1348.

Csikszentmihalyi, M., and Larson, R. (2014). Flow and the Foundations of Positive Psychology (Springer), pp. 35–54.

Davey, J., Cornelissen, P.L., Thompson, H.E., Sonkusare, S., Hallam, G., Smallwoo, J., and Jefferies, E. (2015). Automatic and controlled semantic retrieval: TMS reveals distinct contributions of posterior middle temporal gyrus and angular gyrus. J. Neurosci. *35*, 15230–15239, https://doi.org/10.1523/JNEUROSCI.4705-14.2015.

Dixon, M.L., De La Vega, A., Mills, C., Andrews-Hanna, J., Spreng, R.N., Cole, M.W., and Christoff, K. (2018). Heterogeneity within the frontoparietal control network and its relationship to the default and dorsal attention networks. Proc. Natl. Acad. Sci. U S A *115*, E1598–E1607.

Dosenbach, N.U., Fair, D.A., Miezin, F.M., Cohen, A.L., Wenger, K.K., Dosenbach, R.A., Fox, M.D., Snyder, A.Z., Vincent, J.L., Raichle, M.E., et al. (2007). Distinct brain networks for adaptive and stable task control in humans. Proc. Natl. Acad. Sci. U S A *104*, 11073–11078, https://doi.org/10.1073/pnas.0704320104.

Duncan, J. (2010). The multiple-demand (MD) system of the primate brain: mental programs for intelligent behaviour. Trends Cogn. Sci. *14*, 172–179.

Ellamil, M., Fox, K.C., Dixon, M.L., Pritchard, S., Todd, R.M., Thompson, E., and Christoff, K. (2016). Dynamics of neural recruitment surrounding the spontaneous arising of thoughts in experienced mindfulness practitioners. Neuroimage *136*, 186–196.

Fleeson, W., and Gallagher, P. (2009). The implications of Big Five standing for the distribution of trait manifestation in behavior: Fifteen experience-sampling studies and a meta-analysis. J. Personal. Soc. Psychol. *97*, 1097.

Fox, M.D., Snyder, A.Z., Vincent, J.L., Corbetta, M., Van Essen, D.C., and Raichle, M.E. (2005). The human brain is intrinsically organized into dynamic, anticorrelated functional networks. Proc. Natl. Acad. Sci. U S A *102*, 9673–9678, https://doi.org/10.1073/pnas.0504136102.

Gable, S.L., Hopper, E.A., and Schooler, J.W. (2019). When the muses strike: creative ideas of physicists and writers routinely occur during mind wandering. Psychol. Sci. *30*, 396–404, https://doi.org/10.1177/0956797618820626.

Golchert, J., Smallwood, J., Jefferies, E., Seli, P., Huntenburg, J.M., Liem, F., Lauckner, M.E., Oligschläger, S., Bernhardt, B.C., Villringer, A., et al. (2017). Individual variation in intentionality in the mind-wandering state is reflected in the integration of the default-mode, fronto-parietal, and limbic networks. Neuroimage *146*, 226–235.

Guterstam, A., Björnsdotter, M., Gentile, G., and Ehrsson, H.H. (2015). Posterior cingulate cortex integrates the senses of self-location and body ownership. Curr. Biol. *25*, 1416–1425.

Harmelech, T., and Malach, R. (2013). Neurocognitive biases and the patterns of spontaneous correlations in the human cortex. Trends Cogn. Sci. *17*, 606–615, https://doi.org/10.1016/j.tics.2013.09.014.

Haxby, J.V., Gobbini, M.I., Furey, M.L., Ishai, A., Schouten, J.L., and Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. Science *293*, 2425–2430.

Hektner, J.M., Schmidt, J.A., and Csikszentmihalyi, M. (2007). Experience Sampling Method : Measuring the Quality of Everyday Life (Sage Publications).

Ho, N.S.P., Poerio, G., Konu, D., Turnbull, A., Sormaz, M., Leech, R., Bernhardt, B., Jefferies, E., and Smallwood, J. (2020). Facing up to why the wandering mind: patterns of off-task laboratory thought are associated with stronger neural recruitment of right fusiform cortex while processing facial stimuli. Neuroimage *214*, 116765.

Ho, N.S.P., Wang, X., Vatansever, D., Margulies, D.S., Bernhardt, B., Jefferies, E., and Smallwood, J. (2019). Individual variation in patterns of task focused, and detailed, thought are uniquely associated within the architecture of the medial temporal lobe. Neuroimage *202*, 116045.

Horikawa, T., Tamaki, M., Miyawaki, Y., and Kamitani, Y. (2013). Neural decoding of visual imagery during sleep. Science *340*, 639–642.

Huijser, S., van Vugt, M.K., and Taatgen, N.A. (2018). The wandering self: Tracking distracting self-generated thought in a cognitively demanding context. Conscious Cogn. *58*, 170–185.

Hurlburt, R.T., and Heavy, C.L. (2006). Exploring Inner Experience : The Descriptive Experience Sampling Method (John Benjamins Pub.).

Irish, M. (2019). The Cambridge Handbook of Imagination (Cambridge University Press).

Irish, M., Halena, S., Kamminga, J., Tu, S., Hornberger, M., and Hodges, J.R. (2015). Scene construction impairments in Alzheimer's disease–A unique role for the posterior cingulate cortex. Cortex *73*, 10–23.

Irving, Z.C., and Glasser, A. (2020). Mind-wandering: a philosophical guide. Philos. Compass *15*, e12644.

Jenkins, A.C. (2019). Rethinking cognitive load: a default-mode network perspective. Trends Cogn. Sci. *23*, 531–533.

Jin, C.Y., Borst, J.P., and van Vugt, M.K. (2019). Predicting task-general mind-wandering with EEG. Cogn. Affect. Behav. Neurosci. *19*, 1059–1073.

Kam, J.W., Solbakk, A.-K., Endestad, T., Meling, T.R., and Knight, R.T. (2018). Lateral prefrontal cortex lesion impairs regulation of internally and externally directed attention. Neuroimage *175*, 91–99.

Kamitani, Y., and Tong, F. (2005). Decoding the visual and subjective contents of the human brain. Nat. Neurosci. *8*, 679–685.

Konishi, M., McLaren, D.G., Engen, H., and Smallwood, J. (2015). Shaped by the past: the default mode network supports cognition that is independent of immediate perceptual input. PLoS One *10*.

Karapanagiotidis, T., Vidaurre, D., Quinn, A.J., Vatansever, D., Poerio, G.L., Turnbull, A., Ho, N.S.P., Leech, R., Bernhardt, B.C., Jefferies, E., et al. (2019). The psychological correlates of distinct neural states occurring during wakeful rest. bioRxiv, 2012. 2021.885772 (2020).

Konishi, M., Brown, K., Battaglini, L., and Smallwood, J. (2017). When attention wanders: pupillometric signatures of fluctuations in external attention. Cognition *168*, 16–26.

Konu, D., Turnbull, A., Karapanagiotidis, T., Wang, H.T., Brown, L.R., Jefferies, E., Smallwood, J., et al. (2020). A role for ventromedial prefrontal cortex in self-generated episodic social cognition. Neuroimage *218*, 116977.

Kucyi, A. (2018). Just a thought: how mind-wandering is represented in dynamic brain connectivity. Neuroimage *180*, 505–514, https://doi.org/10.1016/j.neuroimage.2017.07.001.

Kucyi, A., Salomons, T.V., and Davis, K.D. (2013). Mind wandering away from pain dynamically engages antinociceptive and default mode brain networks. Proc. Natl. Acad. Sci. U S A *110*, 18692–18697.

Kucyi, A., Esterman, M., Riley, C.S., and Valera, E.M. (2016). Spontaneous default network activity reflects behavioral variability independent of mind-wandering. Proc. Natl. Acad. Sci. U S A *113*, 13899–13904.

Leech, R., and Smallwood, J. (2019). The posterior cingulate cortex: Insights from structure and function. Handb. Clin. Neurol. *166*, 73–85, https://doi.org/10.1016/B978-0-444-64196-0.00005-4.

Leszczynski, M., Chaieb, L., Reber, T.P., Derner, M., Axmacher, N., and Fell, J. (2017). Mind wandering simultaneously prolongs reactions and promotes creative incubation. Sci. Rep. *7*, 1–9.

Levinson, D.B., Smallwood, J., and Davidson, R.J. (2012). The persistence of thought: evidence for a role of working memory in the maintenance of task-unrelated thinking. Psychol. Sci. *23*, 375–380.

Mar, R.A. (2011). The neural bases of social cognition and story comprehension. Annu. Rev. Psychol. *62*, 103–134.

Margulies, D.S., Ghosh, S.S., Goulas, A., Falkiewicz, M., Huntenburg, J.M., Langs, G., Bezgin, G., Eickhoff, S.B., Castellanos, F.X., Petrides, M., et al. (2016). Situating the default-mode network along a principal gradient of macroscale cortical organization. Proc. Natl. Acad. Sci. U S A *113*, 12574–12579, https://doi.org/10.1073/pnas.1608282113.

Mckeown, B., Strawson, W.H., Wang, H.T., Karapanagiotidis, T., Vos de Wael, R., Benkarim, O., Turnbull, A., Margulies, D., Jefferies, E., McCall, C., et al. (2020). The relationship between individual variation in macroscale functional gradients and distinct aspects of ongoing thought. Neuroimage *220*, 117072.

McVay, J.C., and Kane, M.J. (2012). Drifting from slow to "d'oh!": working memory capacity and mind wandering predict extreme reaction times and executive control errors. J. Exp. Psychol. Learn. Mem. Cogn. *38*, 525.

McVay, J.C., Kane, M.J., and Kwapil, T.R. (2009). Tracking the train of thought from the laboratory into everyday life: an experience-sampling study of mind wandering across controlled and ecological contexts. Psychon. Bull. Rev. *16*, 857–863.

Medea, B., Karapanagiotidis, T., Konishi, M., Ottaviani, C., Margulies, D., Bernasconi, A., Bernasconi, N., Bernhardt, B.C., Jefferies, E., and Smallwood, J. (2018). How do we decide what to do? Resting-state connectivity patterns and components of self-generated thought linked to the development of more concrete personal goals. Exp. Brain Res. *236*, 2469–2481.

Metzinger, T. (2018). Why is mind wandering interesting for philosophers. In The Oxford Handbook of Spontaneous Thought: Mind-Wandering, Creativity, and Dreaming, K. Christoff and K.C.R. Fox, eds. (Oxford University Press), pp. 97–111.

Michel, C.M., and Koenig, T. (2018). EEG microstates as a tool for studying the temporal dynamics of whole-brain neuronal networks: a review. Neuroimage *180*, 577–593, https://doi.org/10.1016/j.neuroimage.2017.11.062.

Mills, C., Raffaelli, Q., Irving, Z.C., Stan, D., and Christoff, K. (2018). Is an off-task mind a freely-moving mind? Examining the relationship between different dimensions of thought. Conscious Cogn. *58*, 20–33.

Miyawaki, Y., Uchida, H., Yamashita, O., Sato, M.A., Morito, Y., Tanabe, H.C., Sadato, N., and Kamitani, Y. (2008). Visual image reconstruction from human brain activity using a combination of multiscale local image decoders. Neuron *60*, 915–929.

Murphy, C., Wang, H.T., Konu, D., Lowndes, R., Margulies, D.S., Jefferies, E., Smallwood, J., et al. (2019a). Modes of operation: a topographic neural gradient supporting stimulus dependent and independent cognition. Neuroimage *186*, 487–496.

Murphy, C., Poerio, G., Sormaz, M., Wang, H.T., Vatansever, D., Allen, M., Margulies, D.S., Jefferies, E., Smallwood, J., et al. (2019b). Hello, is that me you are looking for? A re-examination of the role of the DMN in off-task thought. BioRxiv, 612465.

Murphy, C., Jefferies, E., Rueschemeyer, S.A., Sormaz, M., Wang, H.T., Margulies, D.S., and Smallwood, J. (2018). Distant from input: evidence of regions within the default mode network supporting perceptually-decoupled and conceptually-guided cognition. Neuroimage *171*, 393–401.

Niedźwieńska, A., and Kvavilashvili, L. (2018). Reduced mind-wandering in mild cognitive impairment: testing the spontaneous retrieval deficit hypothesis. Neuropsychology *32*, 711.

Nisbett, R.E., and Wilson, T.D. (1977). Telling more than we can know: verbal reports on mental processes. Psychol. Rev. *84*, 231.

Noonan, K.A., Jefferies, E., Visser, M., and Lambon Ralph, M.A. (2013). Going beyond inferior prefrontal involvement in semantic control: evidence for the additional contribution of dorsal angular gyrus and posterior middle temporal cortex. J. Cogn. Neurosci. *25*, 1824–1850.

O'Callaghan, C., Shine, J.M., Hodges, J.R., Andrews-Hanna, J.R., and Irish, M. (2019). Hippocampal atrophy and intrinsic brain network dysfunction relate to alterations in mind wandering in neurodegeneration. Proc. Natl. Acad. Sci. U S A *116*, 3316–3321.

Pascual-Marqui, R.D., Michel, C.M., and Lehmann, D. (1995). Segmentation of brain electrical activity into microstates: model estimation and validation. IEEE Trans. Biomed. Eng. *42*, 658–665, https://doi.org/10.1109/10.391164.

Poldrack, R.A. (2008). The role of fMRI in cognitive neuroscience: where do we stand? Curr. Opin. Neurobiol. *18*, 223–227.

Raichle, M.E., MacLeod, A.M., Snyder, A.Z., Powers, W.J., Gusnard, D.A., and Shulman, G.L. (2001). A default mode of brain function. Proc. Natl. Acad. Sci. U S A *98*, 676–682, https://doi.org/10.1073/pnas.98.2.676.

Richter, F.R., Cooper, R.A., Bays, P.M., and Simons, J.S. (2016). Distinct neural mechanisms underlie the success, precision, and vividness of episodic memory. Elife *5*, e18260.

Rosenberg, M.D., Scheinost, D., Greene, A.S., Avery, E.W., Kwon, Y.H., Finn, E.S., Ramani, R., Qiu, M., Constable, R.T., and Chun, M.M. (2020). Functional connectivity predicts changes in attention observed across minutes, days, and months. Proc. Natl. Acad. Sci. U S A *117*, 3797–3807, https://doi.org/10.1073/pnas.1912226117.

Rummel, J., and Boywitt, C.D. (2014). Controlling the stream of thought: working memory capacity predicts adjustment of mind-wandering to situational demands. Psychon. Bull. Rev. *21*, 1309–1315.

Schilbach, L., Eickhoff, S.B., Rotarska-Jagiela, A., Fink, G.R., and Vogeley, K. (2008). Minds at rest? Social cognition as the default mode of cognizing and its putative relationship to the "default system" of the brain. Conscious Cogn. *17*, 457–467, https://doi.org/10.1016/j.concog.2008.03.013.

Schooler, J.W. (2002). Re-representing consciousness: Dissociations between experience and meta-consciousness. Trends Cogn. Sci. *6*, 339–344.

Seli, P., Cheyne, J.A., Xu, M., Purdon, C., and Smilek, D. (2015). Motivation, intentionality, and mind wandering: implications for assessments of task-unrelated thought. J. Exp. Psychol. Learn. Mem. Cogn. *41*, 1417.

Seli, P., Risko, E.F., and Smilek, D. (2016). On the necessity of distinguishing between unintentional and intentional mind wandering. Psychol. Sci. *27*, 685–691, https://doi.org/10.1177/0956797616634068.

Seli, P., Ralph, B.C., Konishi, M., Smilek, D., and Schacter, D.L. (2017). What did you have in mind? Examining the content of intentional and unintentional types of mind wandering. Conscious Cogn. *51*, 149–156.

Sestieri, C., Corbetta, M., Romani, G.L., and Shulman, G.L. (2011). Episodic memory retrieval, parietal cortex, and the default mode network: functional and topographic analyses. J. Neurosci. *31*, 4407–4420.

Shamloo, F., and Helie, S. (2016). Changes in default mode network as automaticity develops in a categorization task. Behav. Brain Res. *313*, 324–333.

Smallwood, J. (2013). Distinguishing how from why the mind wanders: a process-occurrence framework for self-generated mental activity. Psychol. Bull *139*, 519–535, https://doi.org/10.1037/a0030010.

Smallwood, J., and Andrews-Hanna. (2013). J. Not all minds that wander are lost: the importance of a balanced perspective on the mind-wandering state. Front. Psychol. *4*, 441.

Smallwood, J., and Schooler, J.W. (2015). The science of mind wandering: empirically navigating the stream of consciousness. Annu. Rev. Psychol. *66*, 487–518.

Smallwood, J., Beach, E., Schooler, J.W., and Handy, T.C. (2008). Going AWOL in the brain: mind wandering reduces cortical analysis of external events. J. Cogn. Neurosci. *20*, 458–469.

Smallwood, J., Gorgolewski, K.J., Golchert, J., Ruby, F.J., Engen, H., Baird, B., Vinski, M.T., Schooler, J.W., and Margulies, D.S. (2013). The default modes of reading: modulation of posterior cingulate and medial prefrontal cortex connectivity associated with comprehension and task focus while reading. Front. Hum. Neurosci. *7*, 734, https://doi.org/10.3389/fnhum.2013.00734.

Smallwood, J., Karapanagiotidis, T., Ruby, F., Medea, B., de Caso, I., Konishi, M., Wang, H.T., Hallam, G., Margulies, D.S., and Jefferies, E. (2016). Representing representation: integration between the temporal lobe and the posterior cingulate influences the content and form of spontaneous thought. PLoS One *11*, e0152272, https://doi.org/10.1371/journal.pone.0152272.

Smallwood, J., Nind, L., and O'Connor, R.C. (2009). When is your head at? An exploration of the factors associated with the temporal focus of the wandering mind. Conscious Cogn. *18*, 118–125.

Smallwood, J., Ruby, F.J., and Singer, T. (2013). Letting go of the present: mind-wandering is associated with reduced delay discounting. Conscious Cogn. *22*, 1–7.

Sormaz, M., Murphy, C., Wang, H.T., Hymers, M., Karapanagiotidis, T., Poerio, G., Margulies, D.S., Jefferies, E., and Smallwood, J. (2018). Default mode network can support the level of detail in experience during active task states. Proc. Natl. Acad. Sci. U S A *115*, 9318–9323.

Spreng, R.N., Mar, R.A., and Kim, A.S. (2009). The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: a quantitative meta-analysis. J. Cogn. Neurosci. *21*, 489–510.

Stawarczyk, D., Majerus, S., Maj, M., Van der Linden, M., and D'Argembeau, A. (2011). Mind-wandering: phenomenology and function as assessed with a novel experience sampling method. Acta Psychol. *136*, 370–381.

Stawarczyk, D., Majerus, S., Maquet, P., and D'Argembeau, A. (2011). Neural correlates of ongoing conscious experience: both task-unrelatedness and stimulus-independence are related to default network activity. PLoS One *6*.

Stawarczyk, D., Cassol, H., and D'Argembeau, A. (2013). Phenomenology of future-oriented mind-wandering episodes. Front. Psychol. *4*, 425.

Teasdale, J.D., Proctor, L., Lloyd, C.A., and Baddeley, A.D. (1993). Working memory and stimulus-independent thought: Effects of memory load and presentation rate. Eur. J. Cogn. Psychol. *5*, 417–433.

Trautwein, F.-M., Singer, T., and Kanske, P. (2016). Stimulus-driven reorienting impairs executive control of attention: evidence for a common bottleneck in anterior insula. Cereb. Cortex *26*, 4136–4147.

Tulving, E. (2002). Chronesthesia: Conscious Awareness of Subjective Time (Oxford University Press).

Turnbull, A., Wang, H.T., Murphy, C., Ho, N.S.P., Wang, X., Sormaz, M., Karapanagiotidis, T., Leech, R.M., Bernhardt, B., Margulies, D.S., et al. (2019a). Left dorsolateral prefrontal cortex supports context-dependent prioritisation of off-task thought. Nat. Commun. *10*, 1–10.

Turnbull, A., Wang, H.T., Schooler, J.W., Jefferies, E., Margulies, D.S., Smallwood, J., et al. (2019b). 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., Karapanagiotidis, T., Wang, H.T., Bernhardt, B.C., Leech, R., Margulies, D., Schooler, J., Jefferies, E., and Smallwood, J. (2020). Reductions in task positive neural systems occur with the passage of time and are associated with changes in ongoing thought. Sci. Rep. *10*, 1–10.

Tusche, A., Smallwood, J., Bernhardt, B.C., and Singer, T. (2014). Classifying the wandering mind: revealing the affective content of thoughts during task-free rest periods. Neuroimage *97*, 107–116.

Unsworth, N., and McMillan, B.D. (2014). Similarities and differences between mind-wandering and external distraction: a latent variable analysis of lapses of attention and their relation to cognitive abilities. Acta Psychol. *150*, 14–25.

Vatansever, D., Bzdok, D., Wang, H.T., Mollo, G., Sormaz, M., Murphy, C., Karapanagiotidis, T., Smallwood, J., and Jefferies, E. (2017). Varieties of semantic cognition revealed through simultaneous decomposition of intrinsic brain connectivity and behaviour. Neuroimage *158*, 1–11, https://doi.org/10.1016/j.neuroimage.2017.06.067.

Vatansever, D., Menon, D.K., Manktelow, A.E., Sahakian, B.J., and Stamatakis, E.A. (2015). Default mode dynamics for global functional integration. J. Neurosci. *35*, 15254–15262.

Vatansever, D., Menon, D.K., and Stamatakis, E.A. (2017). Default mode contributions to automated information processing. Proc. Natl. Acad. Sci. U S A *114*, 12821–12826.

Vidaurre, D., Smith, S.M., and Woolrich, M.W. (2017). Brain network dynamics are hierarchically organized in time. Proc. Natl. Acad. Sci. U S A *114*, 12827–12832, https://doi.org/10.1073/pnas.1705120114.

van der Linden, D., Tops, M., and Bakker, A.B. (2020). Go with the flow: a neuroscientific view on being fully engaged. Eur. J. Neurosci. 1–17, https://doi.org/10.1111/ejn.15014.

van Vugt, M.K., and Broers, N. (2016). Self-reported stickiness of mind-wandering affects task performance. Front. Psychol. *7*, 732.

Wang, H.-T., Smallwood, J., Miranda, J., Xia, C., Satterthwaite, T., Bassett, D., Bzdok, D., et al. (2018a). Finding the needle in high-dimensional haystack: a tutorial on canonical correlation analysis. arXiv, preprint arXiv:1812.02598.

Wang, H.-T., Bzdok, D., Margulies, D., Craddock, C., Milham, M., Jefferies, E., Smallwood, J., et al. (2018b). Patterns of thought: population variation in the associations between large-scale network organisation and self-reported experiences at rest. Neuroimage *176*, 518–527.

Wang, H.-T., Ho, N.S.P., Bzdok, D., Bernhardt, B.C., Margulies, D.S., Jefferies, E., and Smallwood, J. (2019). Neurocognitive patterns dissociating semantic processing from executive control are linked to more detailed off-task mental time travel. bioRxiv, 765073.

Witmer, B.G., and Singer, M.J. (1998). Measuring presence in virtual environments: a presence questionnaire. Presence *7*, 225–240.

Yeo, B.T., Krienen, F.M., Sepulcre, J., Sabuncu, M.R., Lashkari, D., Hollinshead, M., Roffman, J.L., Smoller, J.W., Zöllei, L., Polimeni, J.R., Fischl, B., et al. (2011). The organization of the human cerebral cortex estimated by intrinsic functional connectivity. J. Neurophysiol. *106*, 1125–1165.

Zanesco, A.P. (2020). Quantifying streams of thought during cognitive task performance using sequence analysis. Behav. Res. Methods *52*, 2417–2437.

Zedelius, C.M., and Schooler, J.W. (2015). Mind wandering "Ahas" versus mindful reasoning: alternative routes to creative solutions. Front. Psychol. *6*, 834.

Zhang, M., Savill, N., Margulies, D.S., Smallwood, J., and Jefferies, E. (2019). Distinct individual differences in default mode network connectivity relate to off-task thought and text memory during reading. Sci. Rep. *9*, 16220, https://doi.org/10.1038/s41598-019-52674-9.