The neural correlates of ongoing conscious thought

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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 vary 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.
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
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., 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, Kucyi 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...
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). 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.

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 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.
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.

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 cingulate 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 cortex (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 (Smallwood 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 to 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
standing dynamic state-like features of spontaneous thought (Kucyi, 2018; Zanesco, 2020). Karapanagioti-Markov modeling (HMM) and other dynamic approaches have been argued to be important for understanding 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 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 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 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 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 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 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 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 time-varying neural data to be decomposed into state-related patterns.
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...
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 provide 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 dLFPC 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 dLFPC (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 deliberately 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 (McKeeown et al., 2019). 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 sub-networks that are engaged in different types of cognitive state.

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