**The default mode network in cognition: a topographical perspective**

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**Abstract**| The default mode network (DMN) is a set of widely-distributed brain regions in the parietal, temporal and frontal cortex. These regions often show reductions in activity during attention-demanding tasks but increase their activity across multiple forms of complex cognition, many of which are linked to memory or abstract thought. Within the cortex, the DMN has been shown to be located in regions furthest away from those contributing to sensory and motor systems. Here, we consider how our knowledge of the topographic characteristics of the DMN can be leveraged to better understand how this network contributes to cognition and behaviour.

[H1] **Introduction**

The goal of cognitive neuroscience is to understand the physical substrates of cognition. Early investigations were constrained to functional interpretations of brain activity measured using electrophysiological techniques in animal models (see, for example, REF1) and studies of neurological patients with relatively circumscribed patterns of cognitive and affective deficits (see, for example, REF 2). Towards the end of the last century, advances in non-invasive brain imaging techniques such as positron emission tomography 3 and functional magnetic resonance imaging 4 provided the opportunity to image brain activity online as different cognitive states unfolded: modern cognitive neuroscience was born 5.

Modern brain imaging helped us to understand important aspects of our interactions with the environment, such as how the visual cortex progressively encodes complex features of retinal input 6 and how the sensorimotor cortex controls movement 7. A more puzzling legacy of modern neuroimaging, however, was the discovery that there are a set of regions that are distributed across parietal, frontal and temporal cortices that decrease their neural activity during complex attention-demanding tasks 8,9. These relative reductions in activity were called “task deactivations”8and occurred most prominently in posterior medial cortex (pmc) and angular gyrus (AG), regions of inferior frontal gyrus (IFG), the anterolateral middle temporal cortex (MTC) and medial prefrontal cortex (mpfc) 8,9 (**FIG. 1a, b**). These regions became known as the default mode network (DMN) because their behaviour implied a neural baseline from which specific, more attention-demanding states deviate 8 (**FIG 1b**). Researchers later identified a set of regions exhibiting the opposite pattern of activity, increasing their response during attention-demanding tasks 10. These regions became known as the “multiple demand” system 10 and their behaviour as ‘task-positive’11.

At around the time that the DMN was first characterised, other researchers became interested in the regions that make up this network because of their importance in certain psychological domains, particularly those linked to memory12-14. Foreshadowing our later understanding of the significance of the DMN, Nancy Andreasen and colleagues noted that the association between these regions of cortex and memory processes suggested that these regions are implicated in many of the features said to make us human (such as our sense of identity)13. Other researchers highlighted associations between the DMN and conceptual processing14, or, our sense of self15.

This Perspective considers the diverse roles that the DMN plays in cognition in the context of recent observations regarding its spatial location on the cortical mantle16. In particular, we consider the possibility that the contribution of the DMN to cognition relates to its physical and functional distance from sensory and motor systems 16. The manner with which the cortex has expanded during human evolution 17, has led to the creation of regions of cortex that are less constrained by external input than are regions of sensory-motor cortex involved directly in perception and action 18. It has been suggested that this may have allowed regions in the DMN to take on roles that are both more complex and less directly influenced by the external environment than regions of the cortex that are more directly constrained by extrinsically driven neural activity 18. At the same time, others have noted that locations on the cortical mantle where neural activity is less constrained by external input, may also reflect the natural endpoint of processing streams that function to encode increasingly abstract features of external input and that are hypothesised to allow behaviour to be controlled in an increasingly complex manner 19. In this Perspective we argue that recognizing the topographic location of the DMN provides two important insights into its role in cognition. First, the increased cortical distance between the DMN and sensory systems explains why these regions often seem to operate in a manner that is unrelated to the external environment. Second, the location of the DMN at the ends of processing streams that begin in the cortical periphery offers a mechanism for its involvement in in multiple features of higher-order cognition, often in an abstract manner (e.g. social cognition, semantic and episodic memory). Furthermore, this topographic perspective explains why regions with broadly similar functions are located in the regions of cortex that they are.

**[H1] Mapping the default mode network**

Although the DMN was first identified by measuring its activity during tasks (**FIG. 1b**), important advances were made in mapping its structure by studying its intrinsic activity at rest (**FIG. 1a**). For example, research assessing the functional connectivity of brain regions, a metric calculated based on the temporal correlation between neural activity in different regions of the brain, demonstrated that DMN regions show co-ordinated temporal activity at rest 20,21, which is now known to be a defining feature of a large-scale network 22 .

Researchers were also able to use measurements of resting activity to further decompose the DMN (**FIG. 1c**, **d**). Analysis conducted by averaging across different individuals, known as group level analysis, suggested that the DMN was separated into three ‘subsystems’ 23-25: one anchored in lateral temporal, dorsal prefrontal and parietal regions (known as the “dorsal medial subsystem”), a second focused on the medial temporal and lateral parietal cortex (referred to as the “medial temporal subsystem”) and a third that was described as “engaging midline parietal and frontal regions 23-25 (known as the “core” subsystem, **FIG 1c**). Mappings between these different subsystems and different types of function have been suggested in the literature (See below for a discussion on the role of the DMN in higher order thought). More recently, in depth analysis of single individuals at rest 26 and during tasks 27 provided a different perspective. These ‘high resolution’ studies of single individuals suggested that the DMN consists of two separate juxtaposed ‘subnetworks’28 (**FIG. 1d**). Unlike the spatially-distinct subsystems described above, both of these subnetworks are broadly distributed —with each subnetwork including largely the same set of regions — but are organised in a complex interdigitated arrangement. It has been argued that such interdigitation in regions of the cortex allows for the integration of temporal and spatial information29, suggesting that the discovery of this fine-grained structure may provide a clue as to the mechanism through which the DMN contributes to cognition. It is currently an open question how these different ways of mapping the DMN relate to one another (for discussions see REF 26,28).

Research has also examined the relationship between the DMN and other neural systems. It has been shown that regions showing patterns of brain activity during tasks that are opposite to those of the DMN (for example, increasing activity with task demands) also show a pattern of relatively reduced correlation with regions of the DMN at rest 30. More recently, however, studies that employed multivariate approaches to map neural function established that neural activity within DMN regions, such as the posterior medial cortex, contain signals that relate to neural functioning in diverse systems, including those outside the DMN 31-33. These observations suggested that, as well as forming a cohesive network, the DMN can represent brain activity taking place in other cortical systems, with these representations of activity from within other neural networks often referred to as “echoes”31. These studies, therefore, established that activity in the DMN can also provide information about the activity of task-positive systems, a pattern inconsistent with the classical view of the DMN as being intrinsically isolated from regions that are involved in external goal-directed thought11.

This more complex perspective regarding brain function 34 has been formalised through the application of a class of cortex-wise decomposition techniques, linked to principal components analysis, to measures of brain activity and connectivity 35,36. These approaches generate a series of low dimensional representations of patterns of brain activity distribution across the cortex, that each describe unique patterns of variance in the observed brain activity at rest. These are often referred to as ‘connectivity gradients’ and are based on patterns of covariance within a data matrix. These gradients are ranked based on the percentage of variance that each principal component explains within the initial data (known as explained variance). Within each gradient, brain regions are organised based on the similarity of their observed patterns of activity to each other. In these gradients brain regions grouped at one end have similar fluctuations in activity over time, and collectively show less similarity to the groups of regions at the other end of a dimension (which are also similar in their time courses). In a study that applied this technique to resting brain activity, two of the three connectivity gradients that explained the most variance in activity, and are thus most informative about the organisation of neural function across the cortex, were found to involve the DMN (**FIG. 1e,f**)16. The first gradient (explaining the most variance) revealed that the DMN is most different from regions of unimodal cortex, such that the visual, auditory and motor cortex occupy one end of this dimension, and the DMN occupies the other 16. By contrast, in the third gradient (in terms of variance explained), the regions of the DMN occupy one end of the dimension and the frontal parietal network16, which is thought to coordinate external task states 11, occupies the other end. Analysis of connectivity gradients, therefore, establishes that characterising the intrinsic activity of the DMN as being primarily isolated from, or antagonistic with, that of task-positive systems, does not provide a complete representation of its behaviour. Instead, as we will discuss below, the intrinsic behaviour of the DMN encompasses multiple ‘modes’ of operation, some which are related to external tasks, and others that are not.

**[H1] Roles in higher order cognition**

Important insight into the role of the DMN in cognition has come from researchers who were motivated to investigate its apparent links with memory12,13. These researchers found that DMN activity increases when participants think about themselves15 or engage in certain types of social cognition 37. The DMN was also implicated in imagining events in the future or the past 38 — states known as mental time travel 39 — and in scene construction – the ability to create a spatial scene in imagination 40. Experience sampling studies showed that spontaneous self-generated thought patterns involve many of the features that activate the DMN, including a focus on the self and other people, and episodic representations of events that are not occurring in the immediate environment 41,42. Importantly, these types of experience are common during periods of wakeful rest and decrease in frequency as individuals perform external tasks with increasing demands 43. This may cause what appear to be task-related deactivations in the DMN when complex externally-focused tasks are compared to a resting baseline, or to easy tasks that allow these experiences to occur 43. Consistent with this perspective, the locus of neural activity during periods of active self-generated episodic and social cognition is in the medial prefrontal cortex 44 — a hub of the DMN and a focus of task deactivation8.

In the last two decades a role for the DMN in multiple features of human cognition has been revealed (for meta-analyses see REFs 45-47). These include moral judgement 48-50, empathic responses 51, aesthetic judgement 52, movie watching and narrative comprehension 53-55, spatial navigation 56 and reward-based decision making 57. A number of accounts of the functions of regions of the DMN in specific types of cognition have been suggested. For example, the angular gyrus and posterior medial cortex, both regions of the core DMN subsystem described above, have been suggested to support the retrieval of autobiographical information58. On the other hand, a left-lateralized temporal-frontal “semantic network” 59, anchored by the middle temporal cortex and the left angular gyrus — corresponding broadly to the dorsal medial subsystem of the DMN — has been proposed to allow long term knowledge to help us make sense of the world. Similarly, a “mentalizing network” 60,61 has been identified that includes the right angular gyrus as well as the medial prefrontal cortex (both regions within the core DMN) and is important for social cognition. Finally, the DMN has collectively been suggested to play a role in affective processing, and in particular in the contextualisation of simple affective signals within complex emotionally-laden experiences 62.

Although these perspectives offer valuable accounts of the data connecting DMN activity to function within a given psychological domain, they also raise questions about the nature of the more general contribution that the DMN makes to cognition. **Supplementary Figure 1** shows the results of a meta-analysis of the functional profile of each region within the DMN, based on data available in the Neurosynth database63 (<https://neurosynth.org/>, see also **Supplementary Methods**).This analysis suggests that regions of the DMN are engaged across multiple, apparently distinct, psychological domains (episodic, linguistic, social and emotional). Two DMN regions —the right angular gyrus and the left middle temporal cortex — appear to exhibit the most functionally specific profiles as they are implicated in only two of these domains. Other regions, such as the medial prefrontal cortex have a more general cognitive profile, implicated in all domains covered in our analysis. This heterogeneous mapping of function is hard to reconcile with a view of the DMN as contributing to a single privileged psychological domain 64,65. Furthermore, while this meta-analysis supports the role of the DMN in multiple features of cognition across different domains, it also highlights that the same broad regions of cortex are implicated in many different aspects of higher-order cognition, giving rise to questions about why this is the case. It is noted that this meta-analysis of DMN function presented in **Supplementary Figure 1** is included for illustrative purposes only; for more detailed considerations of the functional roles revealed please see REFs 45-47.

Further information about the functional role of the DMN has been provided by studies revealing that activity within this system can reflect how cognition is influenced by the manner in which cognitive processes emerge within the temporal structure of a task. In one paradigm, participants performed a delayed-match-to-sample task in which the location or identity of shapes had to be memorized 66-69. They were intermittently probed to recall the presence or location of one item from prior trials. During this task, DMN regions in parietal (pmc and ag), temporal (mtc) and frontal cortex (ifg) showed greater activity during decision making when the decisions were based on information from a prior trial than when similar decisions were made based on immediate sensory input 66-69. These include regions within the core and dorsal medial subsystems of the DMN. The magnitude of the responses was greater when the stimuli had multiple meaningful features 66, but a response was observed even for simple shapes like triangles and squares 67,68 (**FIG. 2a**). Research has established that this spatial pattern of regional neural responses is task-relevant because people who exhibit this pattern, do better on this task 67. Furthermore, during this delayed match-to-sample task greater activity within a region of posterior medial cortex was associated with self-reports indicating a greater focus on task-relevant detail 70,71. The role of the DMN in delayed-match-to-sample tasks suggests that this system can be more important in a mode when decisions depend on prior experience rather than when they can be made using immediate sensory input, even if the decisions can have similar representational features (e.g. spatial decisions regarding the location of shapes).

A pattern of task-induced neural activity within regions of the DMN is also seen in the “contextual modulation” of judgements of word association (**FIG 2b**)72. In this paradigm, participants made decisions about semantically ambiguous words (such as whether ‘jam’ is related to ‘traffic’ or to a sweet food). On certain trials this decision was preceded by cues linked to the intended association (such as affective cues related to enjoyment or location cues such as supermarket). During decision making prior exposure to both types of cue increased activity in the frontal cortex (mpfc and mfg), parietal cortex (ag and pmc) , when compared to decisions when a single cue was used. These regions encompass regions from both the core and dorsal-medial Subsystems. Contextual priming, therefore, similar to delayed-match-to-sample judgements, establishes that activity within aspects of the DMN during task completion can vary based on prior experience, even when the information upon which the decision is made remains the same.

Finally, one study has shown that activity in several DMN regions increases when participants perform tasks that depend on internal rules or “schema-based behaviour” (**FIG. 2c**)73. The regions involved include parietal (pmc and ag) and frontal cortex (mpfc), regions within the core DMN subsystem. In this study, participants performed a sorting task in which they needed to use a ‘hidden’ perceptual rule that changed unpredictably without their knowledge. Following a rule change, activity in regions of the DMN was reduced during decision making; however, it increased when participants learned the rule and could use it to guide their decisions (known as the “application” phase). Correlated neural activity in both medial temporal lobe regions and other parts of the DMN was linked to better performance during the application phase, highlighting its task relevance 73. Evidence of the DMN in schema-based decision making, highlights a further example of how activity within this system, can be influenced by prior experience even when the stimuli upon which decision-making occurs remain the same.

Viewed collectively, these studies show that alterations in DMN activity can reflect how cognition changes during a task. During delayed matching to sample, DMN activity is high when participants’ choices are guided by information on the prior trial. During the contextual modulation of decisions, DMN activity is higher when decisions are consistent with multiple informational features derived from immediately preceding information. Finally, during schema-based decision making, behaviour is governed by temporary rules which are generated based on accumulating feedback from prior trials within the task. These examples are all broadly consistent with associations between the DMN and memory processes12; however, they extend the scope of these processes that this network serves to include situations more commonly associated with the multiple demand system10, including perceptual matching, working memory and rule-based sorting.

Importantly, these situations vary in their difficulty, indicating that the role of the DMN can transcend task difficulty. In the delayed-match-to-sample task, participants were slower and less accurate in memory-guided decision-making than in the perceptual control condition, violating the notion that DMN activity is always associated with easier conditions 66-69. By contrast, participants were faster and more accurate, when behaviour was based on a rule during schema-based decision-making 73. One question raised by these observations, which extend the scope of the DMN to forms of external goal-orientated cognition, is how to understand links between the DMN and the process of executive control (see **BOX 1**).

**[H1] Accounting for topography**

As outlined above, contemporary neuroscience has implicated the DMN in many different states and tasks. Given the number of these states, it is unclear whether it makes sense to equate its collective behaviour with a single cognitive domain. An alternative is to explore whether the structural or topographical features of the regions that make up the DMN can shed light on its varied functional contributions.

**[H2] The location of the DMN on the cortical mantle**

Regions within the DMN have been shown to be part of a ‘rich club’ — a set of nodes that show stronger connections between each other than with other regions of cortex 74. This arrangement is thought to be supported by the white matter architecture of the cortex 74,75 and to be related to the emergence of different states of distributed neural activity 76. Furthermore, as discussed above, one study 16 has indicated that the DMN falls at the transmodal end of a connectivity gradient that organises neural systems along a spectrum from unimodal to transmodal cortex; consequently, the DMN is maximally divergent from systems such as the primary visual and motor cortex (**FIG 3a,b**). The same study showed that this functional organisation reflects the topography of the cortex because DMN regions are located on the cortical surface at maximal distances from key anchor points in unimodal systems (**FIG. 3c**) 16. As a result, the position of brain regions on the first connectivity gradient is correlated with their physical distance from primary sensory-motor cortex (**FIG. 3d**)16. Topographically, therefore, regions of the DMN are both highly interconnected and located in cortical territory that maximises their distance from unimodal systems, both in terms of the similarity of their activity and their physical distance.

**[H2] The location of the DMN and theories of cortical organisation**

These topographical features of the DMN suggest that its regions are functionally connected, yet separated from sensory inputs and motor outputs, which is consistent with at least two contemporary views of how the cortex is organised. First, the location of the DMN can be related to accounts of how cortical organization influences information integration 19,77,78. Mesulam 19 proposed a topological schema for describing how cortical connectivity underlies the balance between segregated processing streams and integration. In this architecture, unimodal sensorimotor systems at the periphery support concrete mappings between neural function and behaviour and facilitate simple stimulus–response behaviours. By contrast, the progressive integration of neural signals from unimodal regions of cortex towards a transmodal core allows neural patterns to encode general, invariant features which may be important in cognition in a more abstract manner. Axonal tract tracing studies in non-human primates have established the basic features of this architecture by illustrating that sensorimotor signals converge locally before terminating in the association cortex77. Consistent with this notion of convergence of signals from unimodal systems into the DMN, studies in humans have shown that large-scale networks are organised along the cortical surface from unimodal regions to the DMN in an orderly manner16. Together these observation indicate that the DMN can be understood as being located at the end of processing streams that are anchored at the cortical periphery (**FIG 3b and e**).

Second, the specific location of the DMN in regions of cortex that are distant from sensorimotor cortex is consistent with views of how evolution has influenced mammalian cortical expansion. For example, Buckner and Krienen18 have argued that cortical expansion in regions of association cortex has untethered these regions from the constraints of sensory hierarchies and that this has enabled diverse functional associations of these regions, especially in humans. This view is known as the “tethering hypothesis” 18. Consistent with this view, recent work suggests that the DMN is prominent amongst the regions of the cortex that have changed their functional profile over evolution 79 (**FIG. 3f**). Moreover, this analysis suggests that the anterior to posterior functional axis of the DMN seen in adult humans (seen, for example, in the strong temporal correlation between neural activity in the mpfc and pmc) is likely to be a recent evolutionary development since this pattern is reduced in macaques compared to humans 79.

**[H1] Implications for function**

Understanding the topographic location of the DMN is helpful for understanding it’s influence on cognition and behaviour in a number of ways. First, the distributed, yet inter-connected, nature of the DMN may explain why its regions are collectively involved in many different aspects of cognition. Many forms of complex thought are assumed to rely on multiple, distributed, set of processes. For example, both episodic80 and semantic memory59 are assumed to depend on a ‘hub and spoke’ architecture, in which hub regions interact with highly distributed spoke regions, often in sensory-motor cortex. Contemporary accounts of social cognition suggest that it also relies on a widely distributed set of regions that extend beyond a single neural system 81. Finally, views of emotion indicate that it brings together multiple distributed systems, including those involved in language and perception82. These forms of higher-order cognition may rely on the DMN because its location allows it to encode information about brain activity from across the cortex. Consistent with this view, it has been established that, at rest, patterns of neural activity within the DMN predict patterns of neural activity from across the cortex with a high degree of accuracy 83. This and similar observations31-33 demonstrate that the DMN contains information from across the cortex, a feature that would be useful in situations in which cognition is dependent on the coordination of multiple different elements that are themselves distributed throughout the cortex.

Second, the topography of the DMN also explains why this system is often involved in relatively abstract forms of experience 84. Processing streams, such as the ventral visual stream, are arranged such that the regions involved respond to increasingly abstract features of cognition as information passes along the stream 85; if the DMN is located at the end of these streams then it may be important for relatively abstract features of cognition and behaviour. It is well established that the electrical stimulation of regions of unimodal cortex via intracranial electrodes routinely produces self-reports of experience that are often tied to a specific modality86. However, the likelihood that such stimulation elicits subjective reports with concrete features declines in the regions that are most distant from the sensorimotor cortex, such as the DMN87. At the same time, studies have shown that when individuals learn the hidden meaning of ambiguous images neural patterns within the DMN change, while less reorganisation is observed in unimodal cortex 88. Other studies have found that activity in DMN regions is related to relatively abstract features of cognition, such as the level of specificity 71,89-91 or vividness 92,93 of a stimulus. Finally, studies have also shown that during external, goal orientated thought, the DMN represents features of task context, rather than the specific details of the steps needed to achieve a goal94,95. Together, these studies are consistent with the view that, while concrete features of cognition may depend on peripheral brain systems, neural activity within regions of the DMN may reflect more abstract features of cognition. These abstract features do not directly form the basis of experiences, but instead convey higher order information about their characteristics (such as whether the visual input in an ambiguous image is meaningful88).

Third, the relatively isolated nature of the DMN, highlighted by its distance from the sensorimotor periphery, provides an appealing explanation for the relative disconnect between many of the phenomena linked to this system and information in the ‘here and now’. For example, contemporary views of the DMN highlight an involvement in spontaneous cognition44, emotion62, mental time travel 84 and situations in which task-related decisions are enriched by information other than that provided by immediate input (such as delayed matching to sample decisions68). In each of these cases the balance of constraints on cognition and behaviour are relatively biased away from immediate input, and towards internal representations. This pattern of information processing is described as ‘perceptual decoupling’96 and has been argued to be important for our species’ ability to escape the immediate moment and imagine different times and places 97. Consistent with this notion, effective retrieval is accompanied by reduced activity in visual cortex during delayed match to sample decisions67, while memory deficits associated with epilepsy are linked to a failure to reduce activity in a similar set of regions98. It is possible that the topographic location of the DMN, which is argued to free these regions of the cortex from the constraints of sensorimotor regions18, is helpful for creating the conditions that allow types of decoupled cognition (such a memory) to emerge.

**[H1] Conclusion and future directions**

The DMN has proved challenging to understand in part because this system seemed to pose a difficult question: how does a neural system that deactivates during external attention also play a role in complex cognition? In this Perspective, we have described a topographic model in which the DMN is made up of those brain regions that are functionally and anatomically most distant from the sensorimotor periphery and shown that this provides a parsimonious account for what we know about its functions. In particular, it’s location at the end of processing streams provides an appealing explanations for why this system’s functions are both abstract in quality and wide ranging in scope, while its functional and spatial distance from peripheral systems helps explain its role in cognition and behaviour that are often unrelated to the events in the immediate environment. In this way the topography of the DMN explains why it is involved in cognitive states that combine highly abstract features of cognition and that are often only loosely related to the events in the here and now. As discussed below, this perspective also offers a road map to improve our future understanding of the role that the DMN plays in cognition.

One important outstanding question is the mechanistic role through which the DMN contributes to cognition. A topographic perspective is informative in this regard, because both distance and progressive integration have been suggested to be features of cortical hierarchies 99. Based on accounts of progressive integration, for example, activity patterns within the DMN may describe abstract features of ongoing mental content, integrated from across other regions of cortex. Alternatively, representations in the DMN may take on a coarser informational role, similar in certain respects to how brain activity in the medial temporal lobe is assumed to link to cognition (**BOX 1**). Place cells in the hippocampus, for example, describe specific features of a given spatial layout, such as the colour of the corners of a room 100, whereas grid cells, located in the entorhinal cortex, describe features of the relationship between place cells101 (such as whether all the walls are the same colour). In this way, grid cells can provide similar representational information across different situations in which the spatial context has the same broad features, even if they vary in their specific details 102,103. By analogy, DMN regions may represent coarse information about patterns in brain-wide activity that could be similar for many different potential configurations at lower levels of the hierarchy. This could explain why the DMN is involved in many different representational states, that share broad features (such as a reliance on memory) but differ in their specific informational content.

Hierarchies can also shape the temporal dynamics of complex systems. For example, they can stabilise patterns of neural activity, a process which can help integrate disparate distributed information across time104. In this context, the DMN could be involved in a process that helps distributed signals in peripheral cortical regions to occur closer together in time 105, a process that is assumed to happen during memory retrieval 106. Hierarchies are also a core premise of accounts of predictive coding 107,108, which propose that cortical systems are optimised to reduce mismatch between expected and observed patterns of neural activity, a parameter known as “prediction error”. These views argue that complex representations can emerge through the self-organisation of brain activity across a cortical hierarchy 109,110. It is possible, therefore, that activity in the DMN is linked to a cycle of monitoring, and correcting for, the emergence of prediction error across the cortex. In this way neural patterns across the DMN may provide information regarding the degree to which specific brain contexts are predictable, a metric that would be useful, for example, in shifting between exploratory and exploitative modes of foraging behaviour 111. Consistent with this view, studies in non-human primates suggest neurons in the pmc help map the exploration–exploitation trade-off 112. In addition, studies of reinforcement learning, which can be readily characterised by prediction error models 113, identify activity within medial prefrontal regions of the DMN 114. Understanding the DMN in the context of contemporary views of hierarchies, therefore, allows research to exploit well-defined views on how these shape brain activity (through abstract representation, stable dynamics, or prediction error, for example) as hypotheses to shape future investigations of the mechanistic role the DMN plays in human cognition.

A topographic perspective also helps focus experimental work seeking to capture the contribution of the DMN to cognition. Moving forward, it will be important to study the DMN in both naturally occurring, ecologically valid, states and in more constrained task situations.  While studying the brain in controlled situations divorced from broader contextual regularities can facilitate the identification of systems that reflect controlled cognition, the history of the DMN shows that this may be a relatively poor way to identify how processes linked to global features of neural activity are implemented. Complex patterns of ongoing thoughts occur spontaneously at rest 1,2 or in tasks 3,4 and these states can also be experimentally simulated 5. These approaches allow complex, integrated and ecologically valid states to be investigated, since these thought patterns can be mapped onto cognition in the real world 6. However, they are hard to experimentally control and, critically, confound highly integrated states with internal focus. For example, because states of self-reference 7 or prospection 5 increase activity in the DMN, researchers assumed that this system was important for purely internal states, whereas we now know its behaviour is also important for externally cued cognition during tasks (**FIG. 2**). It is therefore critical to complement investigations of ecologically valid states with tasks in which cognition is organised through learning or experience 8-10 as well as situations which use complex external stimuli (such as movies 11 or audiobooks 12) that contain rich evolving semantic contexts. By explicitly understanding the DMN across a broad range of situations that afford integrated modes of operation, it will be possible to build a more generalisable account of this system’s role in cognition 13.

A topographic perspective also offers a novel hypothesis on why patterns of relative deactivation are important characteristics of the DMN. According to this view, the conditions that favour the operation of traditional ‘task-positive’ networks, such as the multiple demand system are those that prohibit the use of long-term knowledge, or information from the task structure, to guide immediate behaviour. For example, experimenters may utilise stimuli without semantic associations and procedures that make behavioural and neural responses unpredictable (such as trial randomisation and temporal jittering of stimulus presentation). Reductions in activity in the DMN under these situations may occur because these paradigms prohibit the brain from relying on information from memory to support behaviour. Furthermore, this phenomenon may be maximised by the location of DMN regions, which —by virtue of their distance from sensory-motor systems — have neural signals that are generally less influenced by incoming information. It is possible that paradigms that emphasise immediate behaviour and that are unrelated to memory create conditions that are maximally distinct from the situations in which the regions in the DMN are collectively most important. Notably, during delayed match to sample decisions (**FIG. 2**), DMN regions increase their response when cognition combines perceptual inputs with information from the prior trial to make a decision (a more difficult form of cognition but one that is less related to input), relative to when the same decision is made based on current perceptual inputs (an easier decision) 66-68. This indicates that deactivation within the DMN when tasks are more difficult is not inevitable and may not occur when complex behaviour is supported by knowledge, an important hypothesis for future work.

We close by noting that the topography of the DMN means that each of its nodes are relatively closer to certain unimodal features of cortex than to others (for example, the middle frontal gyrus is closest to the motor cortex, while the angular gyrus is closest to visual cortex). This observation suggests that the cortex can be divided into a set of mutually exclusive local cortical “fields”, each centred on a region of the DMN (**FIG. 3g**). These cortical fields encompass different regions of unimodal cortex and so offer a potential means to understand the unique contribution that specific nodes of the DMN play in cognition. For example, it is possible that the contribution of specific DMN regions play in higher order cognition is partly constrained by the functions associated with specific unimodal systems with which it is proximal too. For example, the angular gyrus has been argued to reflect a region that integrates auditory and visual input115, a function that could be made possible by the AGs location at the centre of a cortical field between auditory and visual cortex (**FIG. 3c g)**. However, one important exception to this pattern is the auditory cortex which, unlike visual or somatosensory cortex, is notably closer to certain nodes of the DMN (e.g. the inferior frontal gyrus, angular gyrus and middle temporal cortex)116 than are other primary systems. These regions have been shown to be important for language processing in studies examining groups of individuals59 and in single-subject analyses116. It is therefore possible that this proximity to the auditory system allows these regions of the DMN to capitalise on the capacity for language processes to organise cognitive function, perhaps through the vehicle of inner speech. 117

[H1] Data availability

The spatial map data that support the findings of **FIG. 1b** are available in The Open Science Framework, <https://osf.io/nz8gf/>. The brain masks used to obtain the data used in **Supplementary Figure 1** are available in Neurovault, <https://identifiers.org/neurovault.collection:8569>. The source data for **Supplementary Figure 1** are included in the **Supplementary Data**.

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Author contributions

The authors contributed equally to all aspects of the article.

Competing interests

The authors declare no competing interests.

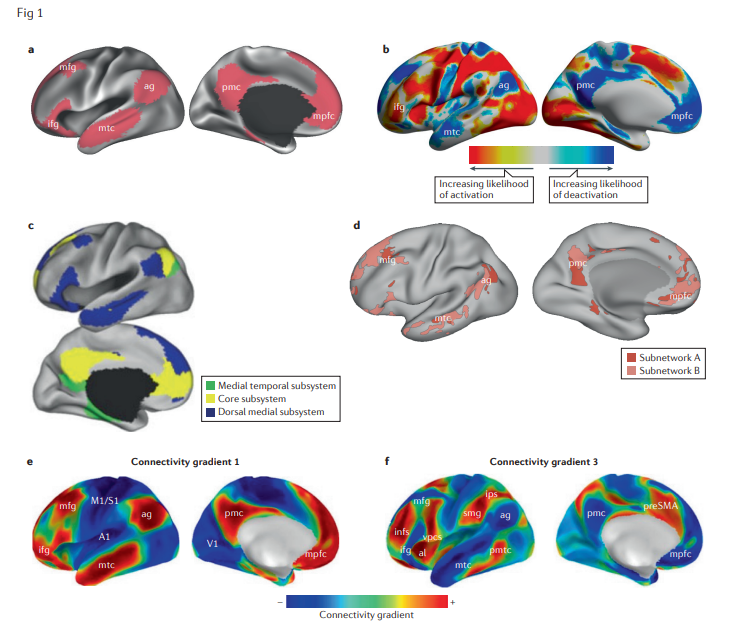
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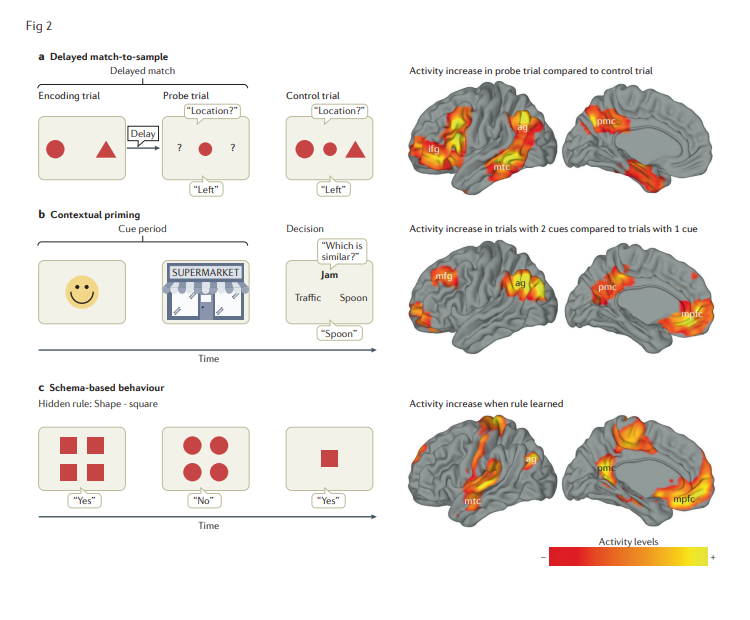
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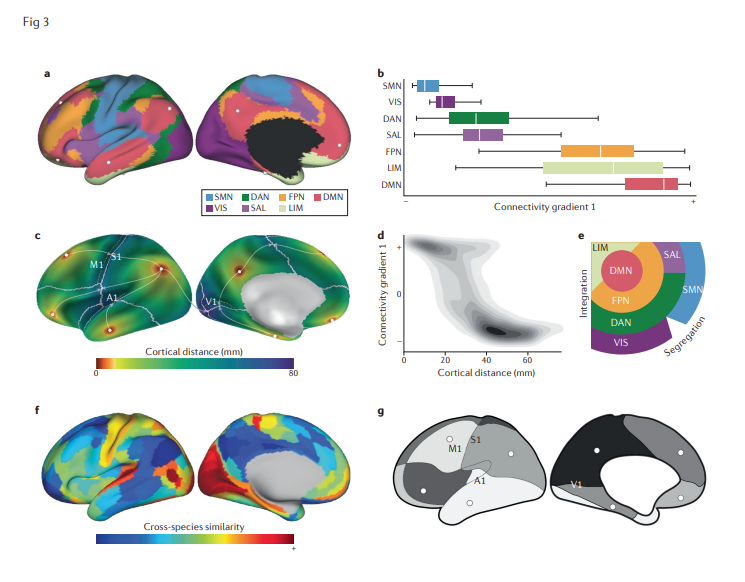
Human Connectome Project: <http://www.humanconnectomeproject.org/>



**Fig 1| Mapping the default mode network (DMN)** **a|** The DMN (coloured pink) is shown as described in a study in which brain regions were parcellated into networks based on the similarity of their temporal neural activity measured at rest24 **b|** The DMN was first discovered through its tendency to deactivate in response to external task demands8. To illustrate this well-established phenomenon, we performed an analysis of patterns of brain activation (defined as. greater activity during tasks relative to baseline) and deactivation (defined as greater activity during baseline than during tasks) using data from the publicly-available analyses performed by the Human Connectome Project118 (http://www.humanconnectomeproject.org/), a large, multi-centre investigation into the organisation of the human brain. In the figure,the colour of a region indicates the percentage of tasks (out of a total selection of 15) for which it was activated or deactivated, compared to their resting baseline (referred to here as its likelihood of activation or deactivation). The regions identified as being more consistently deactivated by tasks include classic DMN regions (as defined by REF 119), such as the posterior medial cortex (pmc), middle temporal cortex (mtc), medial prefrontal cortex (mpfc) and angular gyrus (ag). Please see the Supplementary Materials for further details of how these maps were created. **c,d**| The default mode network has also been further fractionated into ‘subsystems’ and/ or ‘subnetworks’.Group analyses, in which brain activity is averaged across many individuals (**c**) highlighted three subsystems, which are based on statistical groupings of the observed brain activity at rest. 25. By contrast, the results of intensive scanning of single individuals for several hours (**d**) have highlighted two distinct yet adjacent networks with a complex interdigitated structure, based on patterns of correlated brain activity 26. **e,f|** A number of connectivity gradients (of which two are shown here) have been calculated 16 using resting data from the Human Connectome Project118. In these images, regions represented using colours that are closer together show greater correlation with each other over time than regions with colours further apart on the colour spectrum. In these gradients the +/- indicate the different ends of these dimensions, however, the assignment to a specific end of a dimension is arbitrary. In connectivity gradient 1 (**e**), regions with warmer colours include the hubs of the DMN, while regions in cooler colours include sensorimotor cortex (M1/S1), auditory cortex (A1) and visual cortex (V1). This indicates that, for this connectivity gradient, the DMN’s activity differs most from that of unimodal regions16. By contrast, in connectivity gradient 3 (**f**) many of the regions that are recruited when goal orientated cognition occurs (such as the intraparietal sulcus (ips), supramarginal gyrus (smg), ventral precentral sulcus (vpcs), inferior frontal sulcus (infs) and anterior insula (aI), see REF 11) are located towards one end of the gradient, while regions of the DMN are located towards the other end. ifg: inferior frontal gyrus; mfg, middle frontal gyrus; preSMA, pre supplementary motor area; sfg: superior frontal gyrus. Part a is adapted with permission from Yeo et al., 2011. Part c is adapted with permission from Andrews-Hanna et al., 2014. Part d is adapted with permission from Braga et al., 2017. Parts e and f are adapted with permission from Margulies et al., 2016.



**Fig 2| Default mode network (DMN) activity is sensitive to the temporal structure of cognition during a task.** Emerging insight into the role of the DMN in cognition comes from recent studies in which this system’s activity can be related to the specific periods within a task when prior experience contributes to the broader goal of external task completion. In this figure the regions indicated in red or orange show significant activation in the relevant contrast as established in the cited studies. For ease of viewing all of the spatial maps shown in the original studies have been projected onto a standard, non-inflated, MNI 152 template. Please note that, while this allows comparison across the maps presented in this figure, the appearance of the patterns of brain activity may differ from those in the original papers. **a|** Regions of the DMN are activated during delayed match-to-sample decisions. In this task participants must encode information related to the location or identity of shapes (encoding trials) and then make decisions based on this information (probe trials). When neural activity during the probe trials is compared to activity during control trials (in which all the information necessary for the decision is present on screen) regions of parietal (pmc and ag), frontal (ifg) and temporal cortex (mtc) within the DMN show greater activity67. **b|** A broadly similar network is activated when participants make simple associative judgements following contextual priming by multiple cues.In this task participants are exposed to affective and spatial information during a cuing phase and then are subsequently asked to make similarity judgements in a domain that is related to the cues. When decisions following exposure to multiple cues are compared to the same decision with only one cue, greater activity is observed in regions of parietal (ag), temporal (mtc) and prefrontal regions (mfg and mpfc)72. Note that during contextual priming brain activity is also seen in the right middle temporal cortex (not shown)72. **c|** In a schema-based decision making73 task, participants are asked to sort sets of stimuli based on a hidden rule (such as their colour, shape or size). When participants have learnt the hidden rule and can use this information to guide decision-making, brain activity increases in frontal (mpfc) and parietal (ag) and temporal (mtc) regions of the DMN relative to situations when the rule was unknown 73. ag: angular gyrus; ifg: inferior frontal gyrus; mtc: middle temporal cortex; mpfc: medial prefrontal cortex; pmc: posterior medial cortex. Part **a** is adapted with permission from Murphy et al., 2019. Part **b** is adapted with permission from Lanzoni et al., 2020. Part **c** is adapted with permission from Vatansever et al., 2017.



**Fig. 3| Topographic properties of the default mode network (DMN).** The DMN has been shown to be functionally and spatially distant from primary sensory and motor networks, dividing the brain into unique cortical fields. **a|** The DMN presented in the context of other large-scale brain networks 24. The different colours correspond to different networks (also shown in panel b) **b|** Graph representing the networks from panel **a** organised along the first connectivity gradient 1 identified in REF 6 (**FIG. 1e**). The +/- indicate the two ends of this dimension of brain activity 16. **c**| The centroid of the regions that make up the DMN (illustrated by the dots on this panel, as well as in panel a) are most distant from regions of unimodal sensory cortex (A1, M1 and S1). In this panel, the colour gradient represents the spatial distance along the cortical surface between the peaks of connectivity gradient 1 in the DMN and other brain regions 16. The gray lines indicate the regions of the cortex that are equidistant to two DMN regions, and the arrows indicate which sensory landmarks each DMN regions is closest to (for example, pmc is equidistant between M1 and V1). **d**| Plotting the distance measure shown in **c** against connectivity gradient 1 reveals that both metrics are correlated, indicating that the functional and physical separation between the DMN and primary systems are related phenomena 16. **e|** The location of the DMN at the end of processing streams (panel **b**) suggests that it may correspond to the hypothesised functional integrative centre of the cortex. The schematic illustrates how the DMN can be thought of as the end of multiple processing streams that originate in sensory-motor cortex, and, thus the functional core of the brain. This diagram is based on a hypothesis described in REF 19 and provides a topological explanation for how the cortex balances the need for segregation between different sensory systems (indicated by their locations on different locations on the circumference of the semi-circle) with the need for progressive integration of information from the periphery to the core (illustrated by the location of different networks at different points on the radius of the semi-circle). **f|** This panel shows the results of an analysis that compared the similarity of whole brain patterns of functional connectivity in macaques and humans. In this figure, regions in warmer colours show a more similar pattern of connectivity with other regions of cortex in humans and macaques, whereas regions in cooler colours show greater difference in connectivity to other regions of cortex when the two species are compared 79. **g|** Based on the spatial location of the peaks of connectivity gradient 1, we propose that the DMN divides the brain into mutually exclusive ‘cortical fields’, each defined by the convergence of a specific set of sensory/motor streams towards a region of the DMN at the centre of each field 24. This idea is schematically illustrated here by showing how the cortex can be divided into local fields based on which region of the DMN an area of cortex is closest to. A1, primary auditory cortex; DAN, dorsal attention network; FPN, fronto parietal network; LIM, limbic network; M1, primary motor cortex; S1, primary somatosensory cortex; SAL, salience network; SMN, somato motor network; V1, primary visual cortex; VIS – visual network. Part a is adapted with permission from Yeo et al., 2011. Parts b,c,d and e are adapted with permission from Margulies et al., 2016. Part f is adapted with permission from Xu et al., 2020.

**Box 1| Default Mode Network (DMN) function in the context of other neural systems**

The topographic perspective on the DMN outlined in this article highlights the need to understand its function in the context of other cortical regions and systems.

*[bH1] Multiple demand cortex.*

Cognitive neuroscience suggests that the goal oriented control of cognition (often known as executive control) is partly implemented by regions of multiple demand cortex, which are often viewed as the apex of a cortical hierarchy that is important for organising behaviour in a goal orientated manner 11,120. These regions seem superficially to be the opposite to the DMN, since they enhance their responses in situations in which tasks become more difficult 121,122. However, there is growing evidence that the two systems can work together. For example, even when neural activity is reduced in the DMN because of increased external task demands, some DMN regions (such as the posterior medial cortex (pmc)) show increased connectivity with regions of the multiple demand cortex 123,124 and support task relevant cognition71. This may also occur during autobiographical planning 125 and in situations in which decisions combine both prior knowledge and task goals 126. It is possible that these interactions are made possible because the multiple demand cortex is spatially fractionated into regions specialised for their interactions with the DMN and those linked to other multiple response regions more closely aligned to the external environment 127,128. Evidence suggests these interactions may be guided by the dorso-lateral prefrontal cortex, which is involved in the hierarchical organisation of behaviour120 (in part through interactions with the basal ganglia 129). Consistent with this view, the regulation of spontaneous off-task thought with respect to the current level of external demands depends on interactions between the dorso-lateral prefrontal cortex, regions of the dorsomedial DMN and the dorsal attention network 70.

*[bH2] Medial temporal lobe (MTL).*

Many processes linked to the hippocampus and parahippocampal gyrus, such as episodic memory and spatial navigation 130, are also linked to activation of the DMN. However the relationship between the DMN and the MTL is complicated 131, with studies of functional connectivity implicating a region of the parahippocampal cortex as being functionally coupled to the DMN 132. The MTL is important in developing sparse invariant representations that are hierarchically organised and provide a method of mapping complex multi-dimensional spaces 133. These were initially viewed as a code for physical space, but are now understood to map multiple sources of information in a coarse, low dimensional manner 103. It has been argued that the hippocampus is important for setting broad cortical contexts based on regularities gained through experience and it is possible that its connections to the DMN are important in this regard 103. Consistent with this view, the ability of the hippocampus to map task spaces depends on recurrent connections with regions of the DMN, such as the medial prefrontal cortex 134. Moreover, recent work has shown that microstructural features within the MTL have independent links to the large scale connectivity gradients that involve the DMN (**FIG. 1e,f**)135. Understanding the relationship between the MTL and the DMN will help understand how the brain represents complex task spaces and shed important light on the hierarchical control of behaviour.