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.

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, REF.[1]) and studies of patients with neurological disorders 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 the parietal, frontal and temporal cortex that decrease their neural activity during complex attention-demanding tasks[8,9]. These relative reductions in activity were called 'task deactivations'[8] and occurred most prominently in the posteromedial cortex

(PMC) and angular gyrus, regions of the inferior frontal gyrus, the anterolateral middle temporal cortex and the 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 characterized, other researchers became interested in the regions that make up this network because of their importance in certain psychological domains, particularly those linked to memory[12–14]. 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 processing[14], or our sense of self[15].

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 mantle[16]. In particular, we consider the possibility that the contribution of the DMN to cognition relates to its physical and functional distance from the 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 sensorimotor 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 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 end point of processing streams that function to encode increasingly abstract features of external input and that are hypothesized 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 sensorimotor 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 multiple features of higher-order cognition, often in an abstract manner (for example, 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.

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
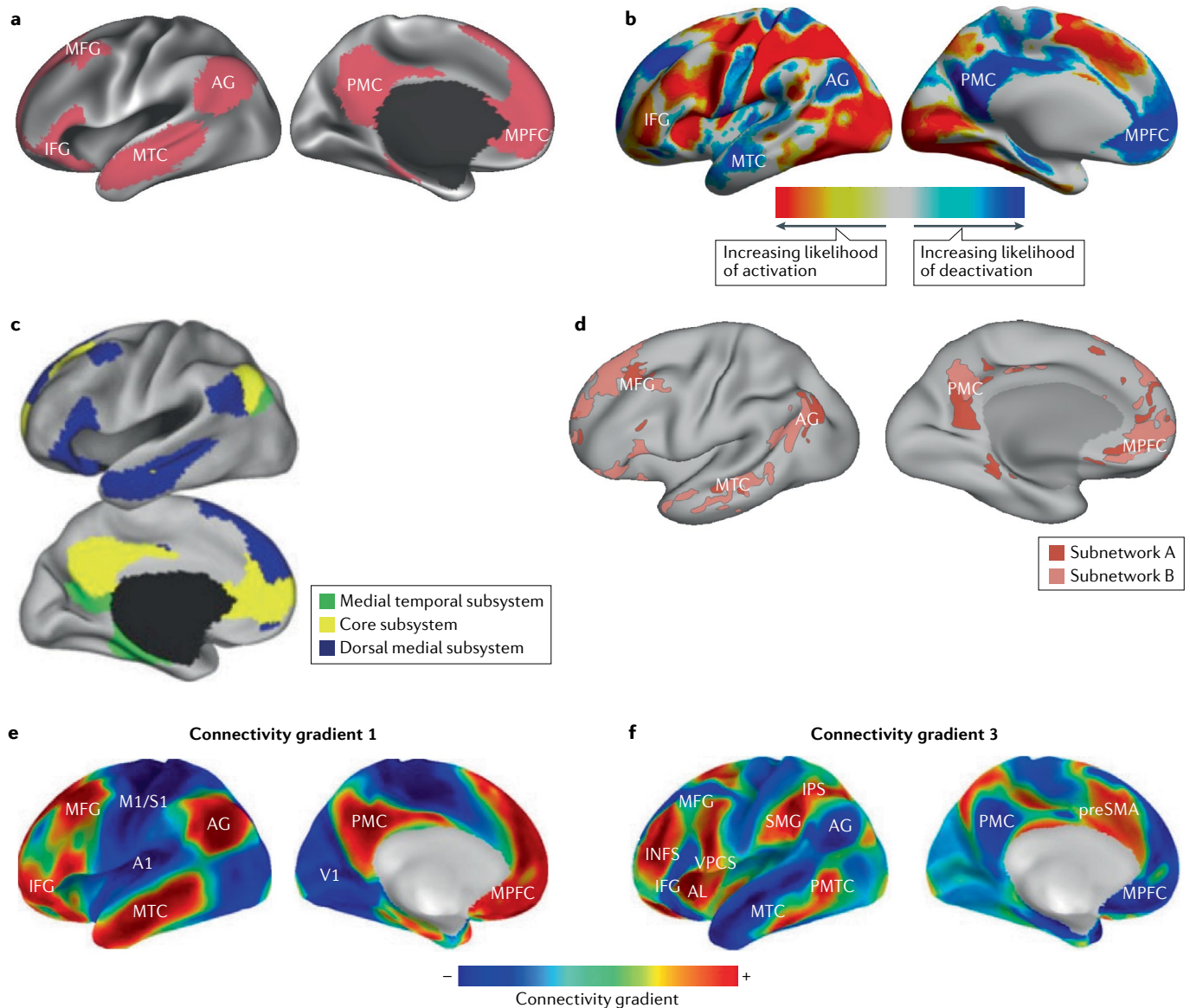
Fig. 1 | **Mapping the DMN. a** | The default mode network (DMN) (pink) as described in a study in which brain regions were parcellated into networks based on the similarity of their temporal neural activity measured at rest[24]. **b** | The DMN was first discovered through its tendency to deactivate in response to external task demands[8]. 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 Project[118] (http://www.humanconnectomeproject.org/), a large, multicentre investigation into the organization of the human brain. Colour of a region indicates the percentage of tasks (out of a total selection of 15) for which it was activated or deactivated, compared with their resting baseline (referred to here as its likelihood of activation or deactivation). Regions identified as being more consistently deactivated by tasks include classic DMN regions (as defined by REF.[8]), such as the posteromedial cortex (PMC), middle temporal cortex (MTC), medial prefrontal cortex (MPFC) and angular gyrus (AG). See Supplementary Methods for further details of how these maps were created. **c,d** | The DMN has also been further fractionated into 'subsystems' and/or 'subnetworks'. Group analyses, in which brain activity is averaged across many individuals (part **c**), highlighted three subsystems, 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 (part **d**) highlighted two distinct yet adjacent networks with a complex interdigi-tated structure, based on patterns of correlated brain activity[26]. **e,f** | Numerous connectivity gradients (of which two are shown here) have been calculated[16] using resting data from the Human Connectome Project[118]. 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, +/– indicate different ends of these dimensions, but the assignment to a specific end of a dimension is arbitrary. In connectivity gradient 1 (part **e**), regions with warmer colours include the hubs of the DMN, whereas regions in cooler colours include the 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 regions[16]. By contrast, in connectivity gradient 3 (part **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), intermediate frontal sulcus (INFS) and anterior insula (AI), see REF.[11]) are located towards one end of the gradient, whereas regions of the DMN are located towards the other. IFG, inferior frontal gyrus; MFG, middle frontal gyrus; preSMA, pre-supplementary motor area; PMTG, posterior middle temporal cortex. Part **a** adapted with permission from REF.[24], American Physiological Society. Part **c** adapted with permission from REF.[25], Wiley © 2014 New York Academy of Sciences. Part **d** adapted from REF.[26], CC BY 4.0 (https://creativecommons.org/licenses/by/4.0/). Parts **e** and **f** adapted with permission from REF.[16], PNAS.

activity in different regions of the brain, demonstrated that DMN regions show coordinated 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 the 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 organized 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 information[29], suggesting that the discovery of this fine-grained structure may provide a clue as to the mechanism through which the DMN contributes to cognition. How these different ways of mapping the DMN relate to one another is currently an open question (for discussions, see REFS[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 PMC, 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 thought[11].

This more complex perspective regarding brain function[34] has been formalized 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 brain activity distribution across the cortex, each describing 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 the explained variance). Within each gradient, brain regions are organized 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 organization of neural function across the cortex, were found to involve the DMN[16] (FIG. 1e,f). The first gradient (explaining the most variance) revealed that the DMN is most different from regions of unimodal cortex, such that the visual, auditory, somatosensory 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 network[16], which is thought to coordinate external task states[11], occupies the other. Analysis of connectivity gradients, therefore, establishes that characterizing 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.

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 memory[12,13]. These researchers found that DMN activity increases when participants think about themselves[15] 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 the 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 with a resting baseline, or 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 MPFC[44] — a hub of the DMN and a focus of task deactivation[8].

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]. Numerous accounts of the functions of regions of the DMN in specific types of cognition have been suggested. For example, the angular gyrus and PMC, both regions of the core DMN subsystem described above, have been suggested to support the retrieval of autobiographical information[58]. 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 MPFC (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 contextualization 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 Fig. 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 database[63] (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 MPFC 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, although 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 noteworthy that this meta-analysis of DMN function presented in Supplementary Fig. 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 the parietal cortex (PMC and AG), temporal cortex (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 such as 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 the PMC 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 (for example, 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[72] (FIG. 2b). 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 middle frontal gyrus) and parietal cortex (angular gyrus and PMC), when compared with 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'[73] (FIG. 2c). The regions involved include the

parietal cortex (PMC and angular gyrus) 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 from 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 that 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 processes[12]; however, they extend the scope of the processes that this network serves to include situations more commonly associated with the multiple demand system[10], 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

a Delayed match to sample
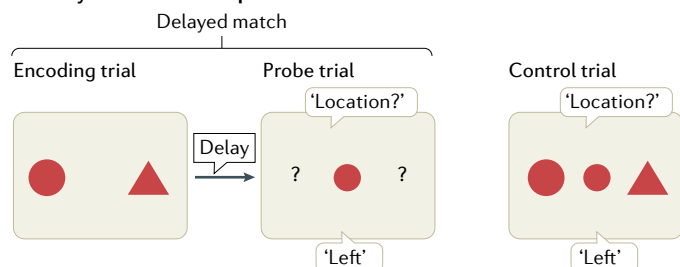
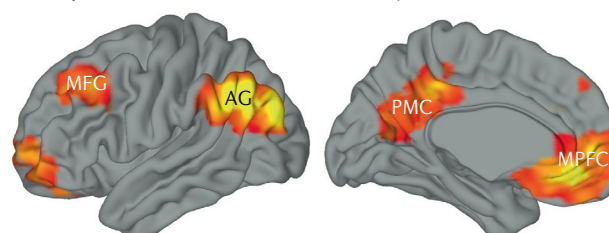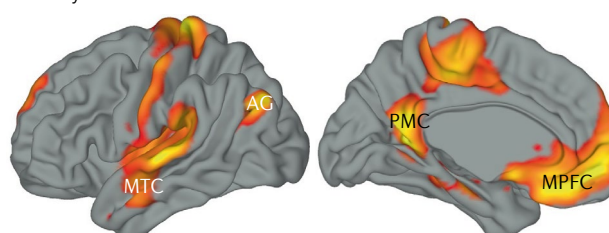**b** Contextual priming
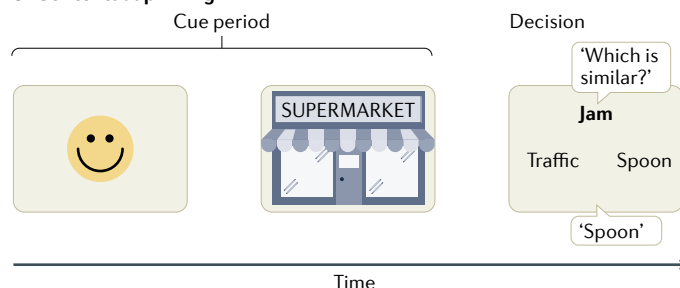
c Schema-based behaviour
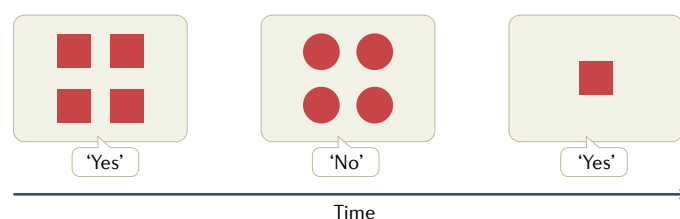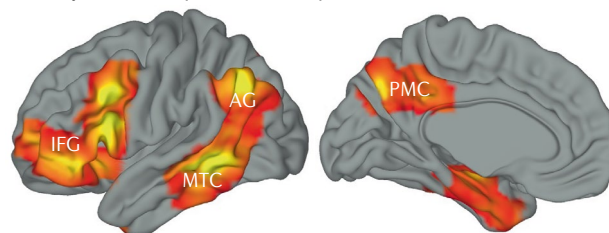
Fig. 2 | **DMN activity is sensitive to the temporal structure of cognition during a task.** Emerging insight into the role of the default mode network (DMN) in cognition comes from recent studies in which this system's activity can be related to the specific periods within a task when prior experience contributes to the broader goal of external task completion. Regions indicated in red or orange show significant activation in the relevant contrast as established in the cited studies. For ease of viewing, all spatial maps shown in the original studies have been projected onto a standard, non-inflated, MNI 152 template. Please note that although this allows comparison across the maps presented here, 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 with activity during control trials (in which all information necessary for the decision is present on screen), regions of parietal cortex (posteromedial cortex (PMC) and angular gyrus (AG)), frontal cortex (inferior frontal gyrus (IFG)) and temporal cortex (middle temporal cortex (MTC)) within the DMN show greater activity[67]. **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 with the same decision with only one cue, greater activity is observed in regions of parietal (AG), temporal (MTC) and prefrontal (middle frontal gyrus (MFG) and medial prefrontal cortex (MPFC)) regions[72]. Note that during contextual priming, brain activity is also seen in the right MTC (not shown)[72]. **c** | In a schema-based decision-making[73] 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), parietal (AG) and temporal (MTC) regions of the DMN relative to situations when the rule was unknown[73]. Part **a** adapted with permission from REF.[67], Elsevier. Part **b** adapted from REF.[72], CC BY 4.0 (https://creativecommons.org/licenses/by/4.0/). Part **c** adapted with permission from REF.[73], PNAS.

DMN and the process of executive control (see BOX 1).

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.

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 the 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 organizes neural systems along a spectrum from unimodal to transmodal cortex; consequently, the DMN is maximally divergent from systems such as the primary visual and primary motor cortex (FIG. 3a,b). The same study showed that this functional organization 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[16] (FIG. 3c). As a result, the position of brain regions on the first connectivity gradient is correlated with their physical distance from the primary sensorimotor cortex[16] (FIG. 3d). Topographically, therefore, regions of the DMN are both highly interconnected and

located in cortical territory that maximizes their distance from unimodal systems, both in terms of the similarity of their activity and their physical distance.

Location of the DMN and theories of cortical organization. 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 organized. 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 that 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 cortex[77]. Consistent with this notion of convergence of signals from unimodal systems into the DMN, studies in humans have shown that large-scale networks are organized along the cortical surface from unimodal regions to the DMN in an orderly manner[16]. Together, these observations 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,e).

Second, the specific location of the DMN in regions of cortex that are distant from the sensorimotor cortex is consistent with views of how evolution has influenced mammalian cortical expansion. For example, Buckner and Krienen[18] 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 as this pattern is reduced in macaques compared with humans[79].

Implications for function

Understanding the topographic location of the DMN is helpful for understanding its influence on cognition and behaviour in numerous ways. First, the distributed, yet interconnected, 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 sets of processes. For example, both episodic[80] and semantic[59] memory are assumed to depend on a 'hub and spoke'

architecture, in which hub regions interact with highly distributed spoke regions, often in the sensorimotor 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 perception[82]. These forms of higher-order cognition may rely on the DMN because its location allows it to encode
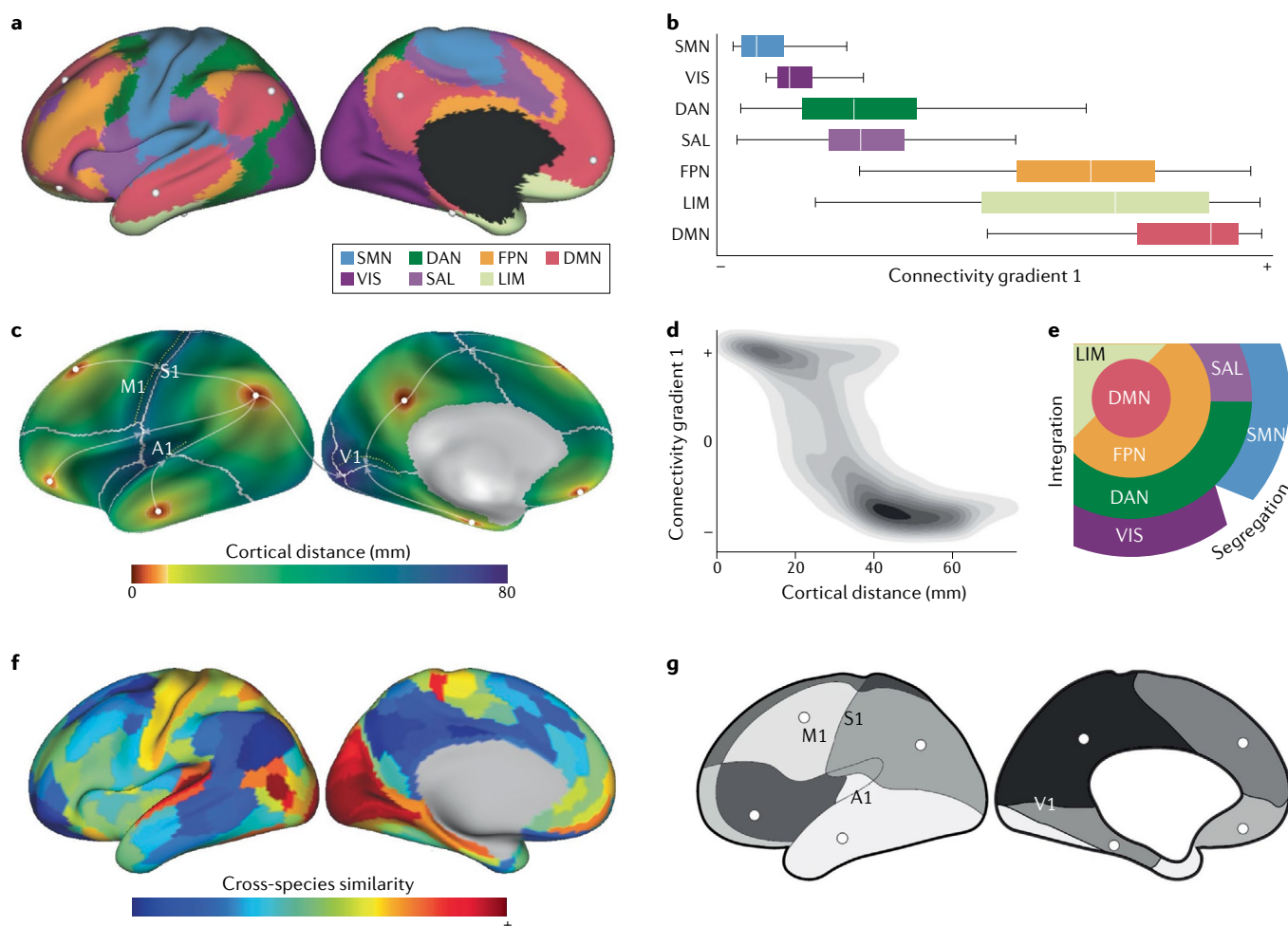
Fig. 3 | **Topographic properties of the DMN.** The default mode network (DMN) has been shown to be functionally and spatially distant from primary sensory and motor networks, dividing the brain into unique cortical fields. **a** | The DMN presented in the context of other large-scale brain networks[24]. Different colours correspond to different networks (also shown in part **b**) **b** | Graph representing the networks from part **a** organized along the first connectivity gradient identified in REF.[6] (FIG. 1e). +/− indicate the two ends of this dimension of brain activity[16]. **c** | The centroid of the regions that make up the DMN (illustrated by dots on this panel, as well as in part **a**) are most distant from regions of unimodal sensory cortex (primary auditory cortex (A1), primary motor cortex (M1) and primary somatosensory cortex (S1)). In this panel, 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]. Grey lines indicate regions of the cortex that are equidistant to two DMN regions, and arrows indicate which sensory landmarks each DMN region is closest to (for example, posteromedial cortex (PMC) is equidistant between M1 and primary visual cortex (V1)). **d** | Plotting the distance measure shown in part **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 (part **b**) suggests that it may correspond to the hypothesized 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

sensorimotor cortex, and thus the functional core of the brain. The 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 points on the circumference of the semicircle) 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 semicircle). **f** | Results of an analysis comparing the similarity of whole brain patterns of functional connectivity in macaques and humans. Regions of warmer colours show a more similar pattern of connectivity with other regions of cortex in humans and macaques, whereas regions of 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 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. DAN, dorsal attention network; FPN, frontoparietal network; LIM, limbic network; SAL, salience network; SMN, somatomotor network; VIS, visual network. Part **a** adapted with permission from REF.[24], American Physiological Society. Parts **b**, **c**, **d** and **e** adapted with permission from REF.[16], PNAS. Part **f** adapted with permission from REF.[79], Elsevier.

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 observations[31–33] 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 modality[86]. 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 DMN[87]. At the same time, studies have shown that when individuals learn the hidden meaning of ambiguous images, the neural patterns within the DMN change, whereas less reorganization 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 goal[94,95]. Together, these studies are consistent with the view that, whereas 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 meaningful[88]).

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 cognition[44], emotion[62], 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 decisions[68]). 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 decisions[67], whereas memory deficits associated with epilepsy are linked to a failure to reduce activity in a similar set of regions[98]. 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 regions[18], is helpful for creating the conditions that allow types of decoupled cognition (such a memory) to emerge.

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, its location at the end of processing streams provides an appealing explanation for why this system's functions are both abstract in quality and wide ranging in scope, whereas its functional and spatial distances from peripheral systems help 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 cells[101] (such as whether all of 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 stabilize patterns of neural activity, a process which can help integrate disparate distributed information across time[104]. 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 optimized 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-organization 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 that neurons in the PMC help map the exploration–exploitation trade-off[112]. In addition, studies of reinforcement learning, which can be readily characterized 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. Although 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, as 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 organized through learning or experience[8–10] as well as situations that 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 generalizable 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 utilize stimuli without semantic associations and procedures that make behavioural and neural responses unpredictable (such as trial randomization 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 maximized by the location of DMN regions, which — by virtue of their distance from sensorimotor systems — have neural signals that are generally less influenced by incoming information. It is possible that paradigms that emphasize immediate behaviour and 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 the cortex than to others (for example, the middle frontal gyrus is closest to the motor cortex, whereas the angular gyrus is closest to the 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, therefore, offer a potential means to understand the unique contribution that specific nodes of the DMN play in cognition. It is possible that the contribution of specific DMN regions in higher-order cognition is partly constrained by the functions associated with specific unimodal systems with which it is also proximal. For example, it has been argued that the angular gyrus is a region that integrates auditory and visual input[115], a function that could be made possible by the location of the angular gyrus at the centre of a cortical field between the auditory cortex and the visual cortex (FIG. 3c,g). However, one important exception to this pattern is the auditory cortex that, unlike the visual or somatosensory cortex, is notably closer to certain nodes of the DMN (for example, 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 individuals[59] and in single-subject analyses[116]. It is therefore possible that this proximity to the auditory system allows these regions of the DMN to capitalize on the capacity for language processes to organize cognitive function, perhaps through the vehicle of inner speech[117].

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 Fig. 1 are available in Neurovault (https://identifiers.org/neurovault.collection:8569). The source data for Supplementary Fig. 1 are included in Supplementary Data.

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PERSPECTIVES

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