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A State-Space Perspective on the Role of the Default Mode Network in Semantic Cognition

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Abstract:

Semantic cognition allows us to understand language, interpret perceptual inputs, retrieve knowledge, and generate meaningful thought. The default mode network (DMN) is often engaged during semantic tasks, yet its precise contribution remains debated, given its involvement in a broad range of cognitive states and domains, including spontaneous thought, autobiographical memory, and social cognition. This review argues that while the DMN's role is difficult to define in traditional psychological terms, it supports several core processes essential for semantic cognition. These include integrating multisensory features, drawing on long-term knowledge to guide thought and perception, and enabling context-appropriate retrieval. The DMN's position in the cortical hierarchy—at a maximal distance from sensory and motor regions—allows it to link diverse sources of information, represent abstract knowledge, and connect flexibly with other large-scale networks. We propose a state space framework to capture how the DMN interacts dynamically with other systems over time, based on intrinsic connectivity patterns. Semantic retrieval occurs in different network states—either when the DMN and executive control networks are co-activated to support effortful search, or when they decouple, with control systems guiding goal-directed retrieval and the DMN supporting more automatic access to knowledge. DMN regions can also couple with and separate from perceptual regions. This framework highlights how dynamic whole-brain states shape the DMN's contributions to semantic cognition across contexts.

Semantic cognition allows us to make sense of the world – enabling us to access concepts flexibly to understand language, recognize objects and faces, use objects correctly, and generate meaningful thoughts [1, 2]. Many studies have observed DMN activation in semantic tasks – including within angular gyrus, posterior cingulate cortex, medial prefrontal cortex and regions in the temporal lobes [3-6], but the computations within this network that are important for semantic cognition are still debated [7, 8]. This review argues that while the DMN's role in cognition cannot be easily defined in psychological terms, it supports key processes that are essential for semantic cognition, including the integration of multisensory features and diverse ideas into coherent conceptual combinations, the use of long-term knowledge to guide both internal thought and perception, and focussed retrieval that is appropriate for the context [9]. The DMN receives inputs from many networks [10, 11] and is thought to be critical for the generation of a variety of distinct whole-brain states: it can couple or separate from executive control and/or sensory-motor regions, supporting diverse semantically-mediated behaviours. We propose a dimensional state-space framework to capture this complex relationship between DMN and other networks to resolve contemporary debates about the role of DMN in (semantic) cognition [12].

Converging evidence that the DMN supports semantic processing

While not all DMN regions are implicated in semantic processing, the DMN strongly overlaps with neuroimaging meta-analyses of semantic tasks in the left hemisphere [Figure 1] [3, 13]. The DMN is often defined using resting-state parcellations of intrinsic connectivity [14], while semantic meta-analyses are based on task contrasts in fMRI, and the amount of overlap between these networks can therefore vary, depending on how they are identified [7, 13]. Convergent evidence for a role of the DMN in semantic cognition is provided by studies showing that individual differences in DMN connectivity predict semantic performance. For example, higher connectivity within the DMN is associated with more efficient retrieval of dominant aspects of knowledge [15], stronger connections between left lateral temporal DMN and medial prefrontal cortex is linked to better reading comprehension [16], and higher semantic aptitude is associated with stronger connectivity between left anterior prefrontal cortex and medial parietal cortex within DMN [17]. At the same time, connectivity between DMN and executive control regions is associated with better summation of weakly-linked meanings [15]. Moreover, focal injury to specific DMN regions can result in semantic deficits: lesion-symptom mapping shows that damage to left angular gyrus (AG) is associated with impaired word comprehension and semantic category fluency [18], often accompanied by a wide range of other spatial, attention and memory functions, consistent with a broad role for this DMN site in cognition [19]. In addition, highly selective degradation of heteromodal conceptual knowledge is associated with bilateral atrophy within the anterior temporal lobes (ATL) in semantic dementia [20]. While the focus of this atrophy lies in ventral temporal regions outside DMN, anterolateral ATL within DMN is affected. In this way, task-based neuroimaging, individual differences in intrinsic connectivity and neuropsychological studies of brain injury all point to the involvement of DMN in semantic cognition.

Both the DMN and semantic network are complex, non-unitary constructs. Fine-grained parcellation can identify distinct subnetworks of the DMN [14, 21; Figure 1]. The “dorsomedial” DMN subsystem, encompassing lateral and anterior temporal lobes, inferior prefrontal regions, left AG, and dorsomedial prefrontal cortex (PFC), shows particularly strong overlap with semantic cognition [21]. The dorsomedial DMN plays a central role in semantic processing, supporting both externally- and internally-focused semantic retrieval, across tasks that engage different input modalities (e.g., words and pictures), task demands (e.g., reading, semantic association, synonym judgment, autobiographical memory), and semantic feature types (e.g., locations and emotions) [11]. This network responds most strongly to abstract, verbal concepts [11]; more marked overlap between meta-analytic maps for semantic cognition and dorsomedial DMN might therefore reflect the dominance of verbal semantic tasks in the literature. Semantic tasks can also activate the medial temporal DMN subsystem associated with scene construction, particularly when scenes and pictures are used to cue semantic retrieval [11, 22]. Core DMN regions in posterior cingulate and AG are engaged when multiple cues or features are integrated, or meanings are retrieved from memory [4-6] [see below]. This subnetwork shows greater activation when participants are more focussed on autobiographical memory retrieval [23, 24]. However, core DMN shows a stronger pattern of task-elicited deactivation than the other DMN subnetworks [11], and some accounts suggest it corresponds to the interdigitation of dorsomedial and medial temporal DMN [25]. These findings, taken together, are consistent with an account of DMN in which subdivisions do not reflect different sources of knowledge about the world (i.e. semantic vs. episodic) but rather different processes (abstraction, scene construction, perceptual engagement vs. decoupling, executive control) that are engaged to differing degrees across semantic and episodic tasks [26, 27]. This view aligns with the component process framework [28, 29], which proposes that memory tasks are supported by flexible combinations of more general cognitive processes. Likewise, semantic cognition emerges from the coordinated recruitment of sets of these processes, rather than a dedicated "semantic system" alone.

Semantic cognition also recruits regions that fall outside of the DMN, for example, in left posterior temporal cortex. Component process accounts of semantic cognition [1, 30, 31] suggest that ATL and/or left AG are critical for integrating different sensory features and aspects of knowledge to form coherent concepts, while left lateral inferior PFC and posterior temporal regions comprise a “semantic control network” associated with controlling patterns of semantic (and episodic) retrieval to suit the context [26, 32]. Left AG shows strong intrinsic connectivity with ATL and medial DMN sites, while left inferior frontal gyrus, which also overlaps with DMN, shows stronger connectivity to posterior temporal regions [33]. This pattern, shown in Figure 1, is consistent with the view that different component processes in semantic cognition draw on different combinations of DMN and other networks. A final crucial difference between semantic networks and DMN concerns laterality [33]: semantic cognition is strongly left lateralised, while DMN is more bilateral (Figure 2). This pattern might reflect the way that semantic cognition often requires DMN to be recruited together with frontoparietal control regions to generate contextually-appropriate semantic cognition -- in the left hemisphere, these networks are more functionally coupled [33, 34].

Functional accounts of role of DMN in semantic processing

While there is no unifying psychological construct to explain the contribution of DMN to semantic cognition, studies highlight a range of semantic contexts that strongly engage this network (Figure 3). These responses are consistent with the location of this network at the top of a processing hierarchy in the human brain that extends from sensory-motor systems, through attention networks and control systems, to DMN [9, 35]. This organisation is reflected by the “principal gradient” of intrinsic connectivity, shown in Figure 3, that captures the functional separation between DMN and unimodal cortex [35].

Deep and sustained semantic cognition: DMN responds when participants process narratives [36]; it shows correlated responses across participants when sentences and paragraphs are presented, but not when participants listen to nonwords or individual words [37]. We recently showed that the transmodal end of the principal gradient is more sensitive to sentence-level and context-dependent semantic variables than lexical-semantic variables pertaining to individual words [38]. This is consistent with a role of DMN in buffering retrieval through time [8, 39].

Semantic integration: AG is linked to combinatorial semantics, when words are used together to establish meanings that are more than the sum of their parts [6], and it shows a stronger response to concepts that have multimodal features [40]. DMN also responds when concepts are interpreted in the context of multiple cues (providing both location and emotion features), compared with when only one of these features is provided (see Figure 3) [4]. These studies suggest that DMN is important for the integration of different sources of information to derive coherent meanings.

Internally-focused semantic cognition: DMN shows more activation when semantic decisions are based on information retrieved from memory, compared with when this information is available in the environment (see Figure 3) [5]. This response pattern is consistent with the role of DMN in internal aspects of thought, including mind-wandering, and autobiographical memory retrieval [23, 41].

Memory-guided semantic decisions and predictions: In many contexts, DMN responds more strongly when meaningful inputs align with our expectations from recent personal experiences and/or the structure of long-term knowledge [26, 42-44]. For example, when participants decide if two verbal concepts share a colour, DMN shows stronger activation when these concepts also share many other features (Figure 3) [44]. DMN can similarly show a larger response to strong associations [26, 45, 46]. This is consistent with the view that DMN supports predictions about the world that are grounded in memory [42, 43].

Tasks that elicit DMN activation may share a ‘family resemblance’ due to this network’s unique anatomical location [9, 35, 47]. Positioned at a maximum geodesic distance from primary sensory-motor systems along the cortical surface [35], the DMN can access a broad range of semantic features and input modalities, rather than being dominated by any one sensory system [9, 48]. This is essential for heteromodal and integrative semantic processing, and supports perceptually decoupled, memory-guided states that can diverge from ongoing experience. This account of the role of DMN also explains the engagement of this network in social cognition, self-related thought, and episodic memory, which are also heteromodal, and/or guided by memory [9, 35, 49]. This account is supported by analyses of individual differences in cortical distance between functional parcels and sensory-motor landmarks; greater distance predicts greater recruitment by meaningful inputs, while greater proximity to sensory-motor regions predicts stronger activation in response to relevant sensory input [50].

Different semantic modes

The anatomy of DMN also allows this network to form hubs that support different connectivity patterns, so that it can couple with memory, control and perceptual regions in different contexts (see Figure 4) [9, 10, 35, 51]. This makes it possible for DMN to support a range of semantic (and other cognitive) “modes” that are sustained by different functional interactions [12, 36, 52, 53], including perceptually coupled versus decoupled retrieval [23, 54], and relatively automatic retrieval of dominant aspects of knowledge versus controlled retrieval of weaker aspects of long-term memory [52, 55]. These modes of retrieval and their associated connectivity patterns can be described within a dimensional framework of brain function, using gradients of intrinsic connectivity that explain the most variance as dimensions of a neural state space (see Figure 4). Connectivity gradients are derived from whole-brain connectivity matrices that capture the time-series correlation between every pair of parcels across the cortex; these matrices are decomposed to identify the dimensions of this data.

Gradient 1 captures the distinction between transmodal DMN and unimodal cortex (the principal gradient above), Gradient 2 relates to the difference between visual and auditory-motor cortex, while Gradient 3 explains the distinction between aspects of DMN and frontoparietal control regions. Since both Gradients 1 and 3 have DMN at one end, they capture distinct functional relationships that this network forms over time.

Perceptual coupling and decoupling: DMN supports perceptually-decoupled retrieval modes in which DMN subsystems are largely connected to each other and insulated from input: this can promote mind-wandering, and autobiographical memory retrieval [23, 56]. DMN is implicated in internally-generated conceptual imagery, together with modality-specific regions [54, 57]. At the same time, DMN supports the comprehension of words and images in contexts like reading that are perceptually coupled [36, 37]. During reading comprehension, DMN shows stronger coupling to visual and motor regions, potentially supporting external engagement [23]. There are parallel patterns of connectivity from visual regions responding to object and scenes to lateral and medial DMN subsystems, implicated in semantic abstraction and scene construction respectively [58]. These visual-to-DMN pathways occupy different parts of state space: semantic categorisation is more transmodal on Gradient 1 and more balanced between modalities on Gradient 2, while scene memory is more unimodal on Gradient 1 and highly visual (see Figure 4). This explains why verbal semantic tasks recruit aspects of DMN that are towards the apex of the principal gradient even when they involve processing visual or auditory input [11].

Automatic vs. controlled semantic cognition: DMN often shows stronger responses to easy semantic tasks in which task goals are highly aligned with the structure of long-term knowledge [26, 59], and in this context, DMN may functionally separate from cognitive control regions [60]. However, parts of DMN also fall within the semantic control network [45]: this network – recruited when non-dominant aspects of knowledge are prioritised to suit the task demands [30] – is juxtaposed between DMN and frontoparietal control regions in the left hemisphere, suggesting a common response across elements of both networks [44, 61]. In this way, DMN can support different patterns of semantic retrieval that bring to the fore the most accessible information in memory, or more unique and creative conceptual associations [45].

These different modes of semantic retrieval help to resolve an ongoing debate in the semantic literature. DMN regions such as left AG often deactivate in response to semantic demands compared with rest [7], consistent with a “task-negative” profile [7]. However, DMN shows a stronger response to semantic than non-semantic tasks, even for relatively demanding judgements [5, 44, 55]. A recent study found that task difficulty and semantic processing make independent contributions to the response in DMN [62], highlighting the complexity of this network’s contributions to cognition. Our dimensional framework can explain why DMN anti-correlates with control regions in some contexts, yet supports the retrieval of goal- and context-relevant aspects of meaning in controlled semantic tasks [55, 63]. DMN shows functional similarity with transmodal frontoparietal control regions on Gradient 1 (see Figure 3), and semantic control regions are located towards the top of this gradient [12, 61], yet DMN also shows functional separation from control networks on Gradient 3 (see Figure 4), for example, when control networks are used to select representations in a goal-directed fashion [12].

In summary, a whole-brain state-space account is useful for explaining the role of DMN in semantic cognition, because distinct dimensions of connectivity can capture the varying functional relationships that DMN shows over time. For example, DMN can be highly connected to and co-recruited with other heteromodal networks during controlled semantic cognition, but it can also functionally separate from the frontoparietal control network, when non-semantic tasks are controlled. Moreover, different subnetworks within DMN may be associated with different dimensions of connectivity: regions of semantic activation in dorsomedial (lateral frontotemporal) and medial temporal DMN subsystems are more strongly connected to the transmodal end of Gradient 1 than deactivating voxels, while the reverse is true for core DMN. Dorsomedial and medial temporal subsystems are also more connected to executive control regions on Gradient 3, while core DMN is more functional separated from control networks, especially for voxels that activate in semantic tasks [11]. In line with these complex functional relationships, DMN shows rapid change in connectivity as the location on the cortical surface changes [64], allowing this network to support a wide range of functional modes that support different aspects of (semantic) cognition.

This perspective generates predictions about where different kinds of semantic tasks might fall within a brain state space defined using connectivity gradients. Patterns of sustained semantic cognition, when inputs align with long-term memory and/or when diverse semantic features are integrated, are expected to engage more transmodal regions along the principal gradient. In contrast, more stimulus-bound tasks involving isolated words or perceptual judgments may fall closer to the unimodal end of Gradient 1. Gradients 1 and 2 may both be relevant to differences between perceptually coupled states (e.g. during reading or picture naming) and perceptually decoupled ones (e.g. during autobiographical reflection or conceptual combination in the absence of input), while Gradient 3 distinguishes between automatic retrieval and goal-driven semantic search. Future work could situate diverse semantic tasks within this low-dimensional space to better understand how different cognitive modes engage the DMN together with other networks.

Conclusion

The brief review confirms a role for the DMN in a family of semantic functions that involve transmodal, memory-guided and integrative cognition. These DMN functions have been linked to its anatomical location at the apex of a processing hierarchy that extends from sensory systems through attention networks and control systems and ending in the DMN. However, DMN regions participate in multiple functional networks, depending on the cognitive context, helping to explain inconsistencies in the literature: for example, DMN's anti-correlation with task demands yet its response during controlled semantic cognition. We propose a dimensional perspective to explain the role of DMN in semantic cognition, in which gradients of intrinsic connectivity capture the different functional relationships that arise between DMN and other networks over time. This framework helps to explain diverse functional responses in DMN.

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This study helps to reconcile contradictory views about the role of angular gyrus in semantic cognition, showing that this region shows both domain-general patterns of deactivation in hard tasks and domain-specific activation in semantic tasks. These different responses support the view that DMN can form different functional relationships with control regions over time.

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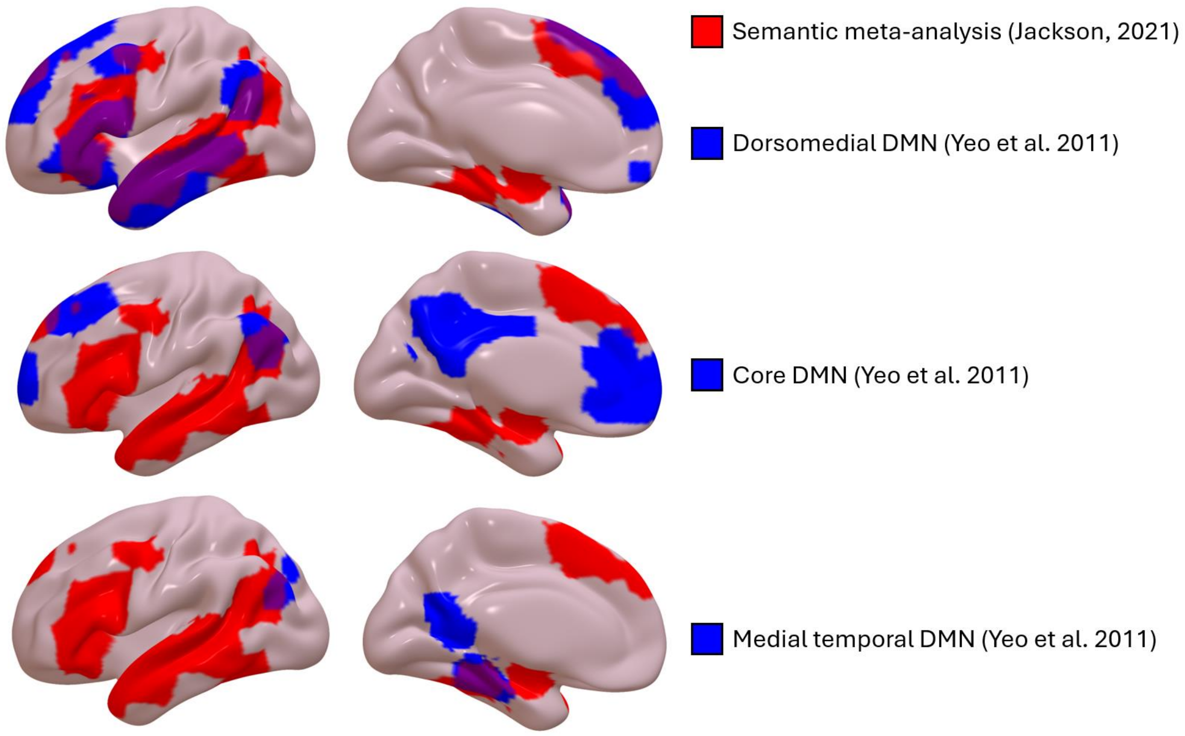

Figure 1: Blue: DMN subsystems, defined by the 17-network parcellation of resting-state fMRI, from Yeo et al. (2011). The three DMN subsystems are overlaid with the semantic meta-analytic map from Jackson (2021) showing brain regions reliably activated by semantic tasks across studies. The dorsomedial DMN is associated with semantic tasks (e.g. Andrews-Hanna et al., 2010) and shows the strongest overlap with the meta-analytic map; however, there is also overlap between semantic processing and DMN in left angular gyrus for core DMN and in left posterior angular gyrus/lateral occipital cortex and medial temporal cortex for the medial temporal DMN subsystem.

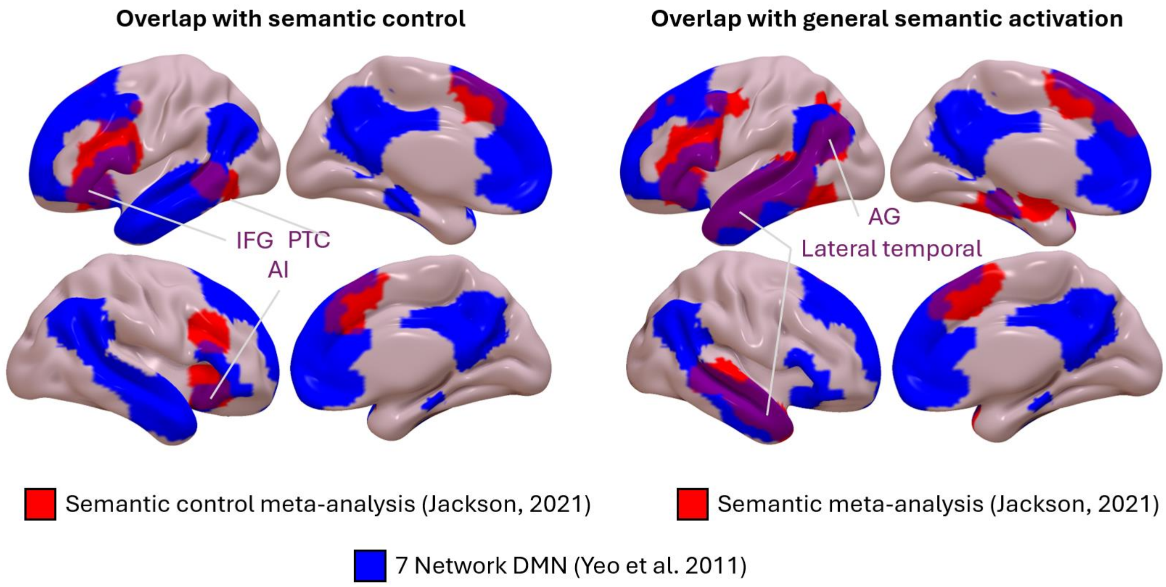

Figure 2: The overlap between DMN and different components of the semantic network. Blue = DMN, defined by the 7 network parcellation from Yeo et al. (2011). Red = semantic meta-analyses from Jackson (2021). Left: DMN overlaps with regions of the semantic control network, which show stronger activation across diverse contrasts of hard over easy semantic decisions, in left IFG (IFG), left posterior temporal cortex (PTC), and right anterior insula (AI). Right: DMN additionally overlaps with regions of the semantic network that fall outside the semantic control network, in left and right lateral temporal cortex and left angular gyrus. Volumetric maps are projected to the surface using Surfice.

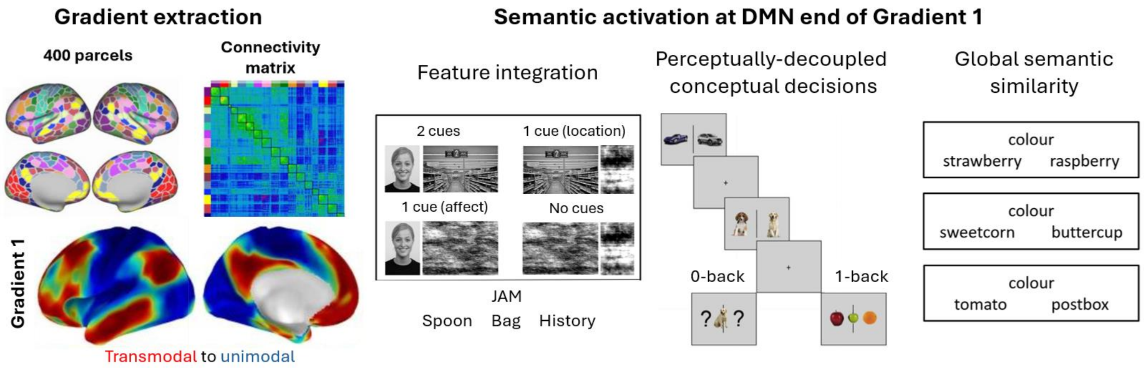

Figure 3: Left: The method used to extract the principal gradient of intrinsic connectivity (reproduced from Wang et al., 2024). The analysis is based on 400 parcels covering the whole cortex. Intrinsic connectivity data recorded using resting-state fMRI is computed for each pair of parcels. This connectivity matrix is then decomposed using diffusion embedding. The component explaining the most variance, Gradient 1, captures the separation in connectivity between transmodal regions in red, and unimodal regions in blue. Right: Examples of semantic paradigms that activate the transmodal end of Gradient 1. Feature integration (Lanzoni et al., 2020): participants see photographs of facial portrayals of emotion or locations, or scrambled versions of these images, prior to semantic decisions about ambiguous words that are disambiguated by these cues. The transmodal end of Gradient 1 shows stronger activation to multiple cues (2 cues > 1 cue), even though there are no behavioural differences between these conditions. Perceptually-decoupled conceptual decisions (Murphy et al., 2018): on 0-back trials, participants decide if a central object is the same category as the object on the left or right of the screen, so that perceptual input guides conceptual matching. On 1-back trials, they decide if a central object is the same category as the object on the left or right of the screen on the previous trial, so that memory guides the conceptual match. The transmodal end of Gradient 1 shows stronger activation to 1-back over 0-back trials, particularly when 1-back decisions involve conceptual rather than colour matching, even though 1-back decisions are harder than 0-back. Global semantic similarity: Wang et al (2020): Participants make decisions about whether two concepts have the same colour, shape or size. The task manipulates the number of task-irrelevant features that overlap. The transmodal end of Gradient 1 shows stronger activation to items with more global semantic similarity, even when concepts are NOT matching on the task-relevant feature, such that global semantic similarity makes the decision harder.

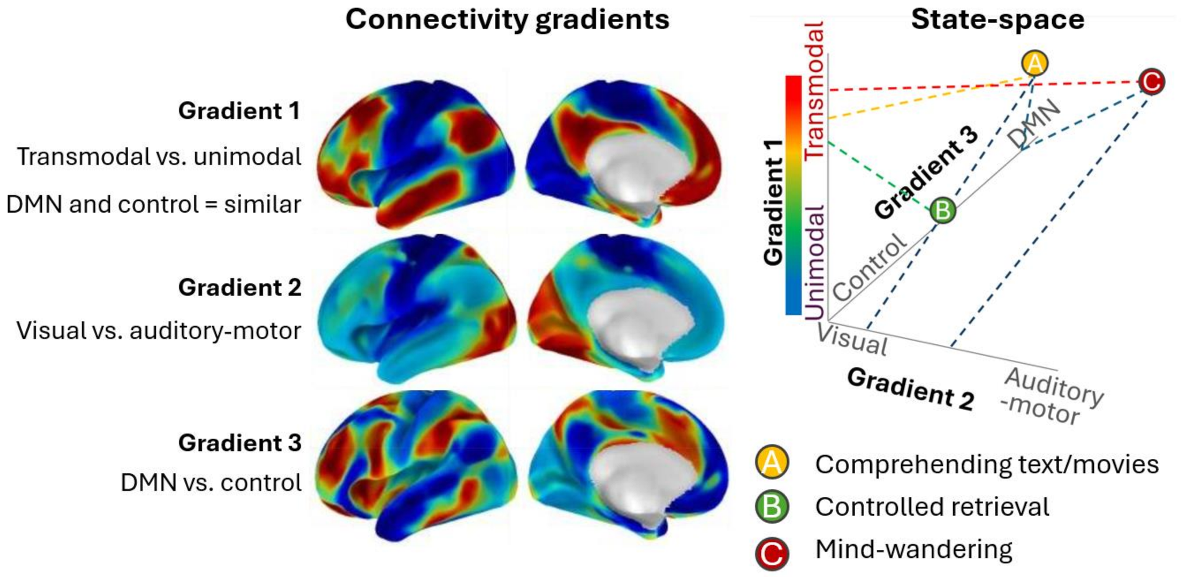

Figure 4: Left: The first three gradients of intrinsic connectivity, extracted from diffusion embedding applied to HCP resting-state fMRI data by Margulies et al. (2016) and replotted. These gradients capture key differences in functional connectivity over time. Right: These gradients can be used to describe the neurocognitive basis of different aspects of semantic cognition (e.g. Wang et al., 2024). For example, A: comprehending text or movies might be sustained by a state that is relatively transmodal on Gradient 1, visual on Gradient 2 and highly dependent on DMN memory systems on Gradient 3. B: Controlled semantic retrieval also recruits brain regions that are transmodal on Gradient 1, and visual on Gradient 2, but more controlled on Gradient 3. Mind-wandering and off-task thought is transmodal on Gradient 1, balanced across different sensory systems on Gradient 2, and highly dependent on DMN memory systems on Gradient 3. In this way, sensory engagement might capture the difference between perceptually coupled and decoupled states (States A vs. C), and the balance of DMN-memory to control networks is associated with semantic ‘flow’ states like movie watching and mind-wandering versus more controlled semantic cognition (States A and C vs. B). These state-space locations are for illustrative purposes and are not based on data analysis.