COMMENTARY

Converging evidence for the role of transmodal cortex in cognition

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The studies by Vidaurre et al. (1) and Vatansever et al. (2) in PNAS provide contrasting, yet complementary insights into the role that regions of transmodal cortex, including those in the default mode network (DMN) (3) and the fronto-parietal network (FPN) (4), play in cognition.

Vatansever et al. (2) used task-based fMRI to illustrate how the DMN and FPN work collectively to guide complex behavior. In their study, participants performed the Wisconsin Card Sorting Task (WCST) (5) while brain activity was measured using fMRI. In this task, participants sort shapes based on features (color, shape, or number). The feature is not revealed to the participant at the outset of a block of trials, and must instead be learned based on feedback presented after each trial. The feedback is used to identify the current feature rule, which is then applied on subsequent trials. Periodically, the rule changes and feedback is used to update the current goal representation. Vatansever et al. (2) demonstrate that the FPN is active after a rule change—the "acquisition phase"—suggesting its involvement in encoding the contingencies upon which the sorting decision is based. In later sections of the block—the "application phase"—when the individual understands the rule, activity within the FPN is reduced, and activity within the DMN increases (Fig. 1*A*). Therefore, the activity within the DMN corresponds to periods when contingencies determining cognitive decisions are established. Additionally, and importantly, Vatansever et al. (2) show that patterns of increased DMN connectivity are also linked to better response latency during correct trials. Together, these results corroborate recent studies showing that the DMN supports external task processing when behavior depends on preexisting representations guiding cognition (6–9).

Using resting-state fMRI data from the Human Connectome Project (10), Vidaurre et al. (1) apply a hidden Markov model (HMM) (11) that exploits the spatiotemporal patterns in activity to infer a number of different brain states. Vidaurre et al. (1) show that the time spent in each state, known as "fractional occupancy," remains consistent across different scanning sessions and is heritable. The ability to use HMMs to identify states based on intrinsic dynamics captured by fMRI constitutes an advance in our ability to characterize the nature of ongoing brain activity, providing an intuitive method for understanding how neurocognitive processing can be understood as a succession of neurocognitive states (12, 13).

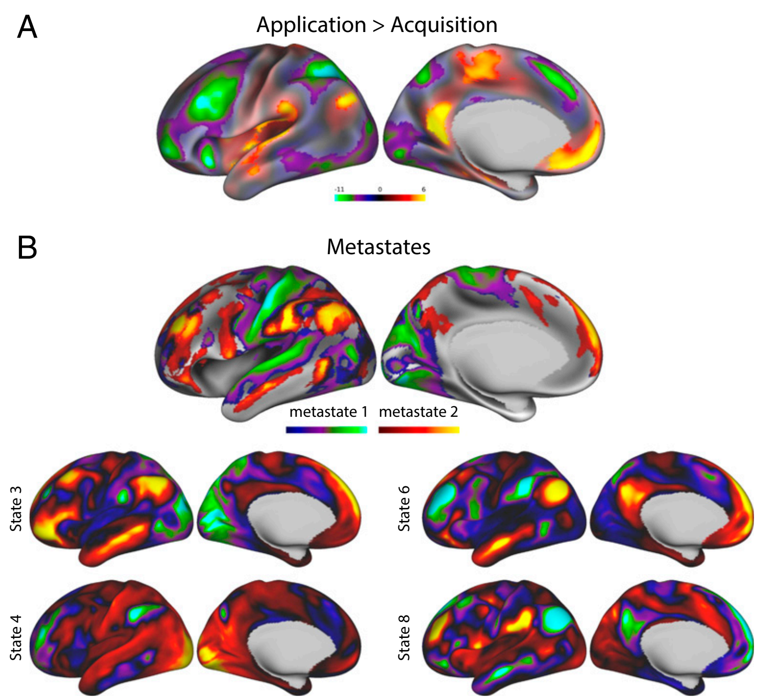

Fig. 1. Brain states demonstrating the active role of the DMN and FPN in cognition. (*A*) Contrast of application versus acquisition phases during performance of the WCST (2). (*B*) Metastates described using a HMM applied to resting-state fMRI data (1), as well as two example states from metastate 1 (*Bottom Left*) and metastate 2 (*Bottom Right*).

One observation emerging from the analysis of Vidaurre et al. (1) is that specific states are hierarchically organized, forming temporal groupings referred to as "metastates." These reflect a dissociation between states anchored by regions of the cortex concerned

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with constrained neural processing (such as the sensorimotor systems), from those anchored by transmodal regions of the cortex, hypothesized to serve more abstract functions (14, 15) (Fig. 1*B*). Vidaurre et al. (1) show that participants spending more time in the transmodal metastate perform better on measures of intelligence, executive control, and processing speed. Crucially, the metastates have a stronger association to behavior than the individual states, indicating that they are functionally relevant above and beyond their constituent elements.

Both studies provide accounts of the transmodal cortex anchored in both neural and psychological measurements (16), and thus constrain accounts of the role that transmodal cortex, and in particular the DMN, plays in cognition. Historically, the DMN was argued to be task-negative, supporting forms of cognition irrelevant to external goals (17), because its activity emerged in simple nondemanding tasks (3), as well as states, such as mind-wandering (18) and attentional lapses (19). However, the links with cognition revealed in these two studies are inconsistent with this account of the DMN.

Vidaurre et al. (1) show that spending time in states anchored in transmodal cortex, including those dominated by the DMN (see state 6 in Fig. 1*B*), predict better executive control and higher intelligence (Fig. 1). Thus, even though brain activity analyzed by Vidaurre et al. (1) takes place at rest, the functional implications of their analysis extend to forms of cognition measured in the context of a task (such as intelligence). A similar conclusion emerges from the study by Vatansever et al. (2). The progression to a state of rule-based behavior in the WCST corresponds to a shift in brain activity from an initial focus in fronto-parietal regions to those in the DMN (Fig. 1*A*). Critically, participants performed the task better in periods when the DMN was more active, and connectivity within this network supported better task performance. Together, both studies highlight the need to move beyond a task-negative account of the DMN in cognition.

Both studies are broadly consistent with an overarching view of the DMN as important when cognition is guided by representations from memory (20). Vatansever et al. (2) found that the DMN is active after participants have acquired the rule in the WCST, corresponding to periods when memory input is most relevant for task performance. Although determining the specific functional processes of the metastates identified by Vidaurre et al. (1) is challenging since they occur at rest, we do note recent studies have linked patterns of integration at rest within both the DMN and FPN as important for different types of spontaneous thoughts (21–25). It is possible, therefore, that the fractional occupancy of the transmodal metastate may reflect types of spontaneous thought that derive their content from memory (26). The hypothesis that the DMN is relevant when cognition requires information from memory can account for many conditions that activate this system. For example, the DMN is active during periods of future thinking (27), semantic decisions that depend on strong conceptual associations (28), mind-wandering (29), moral reasoning (30) and, perhaps most tellingly, during spatial or numerical decisions made based on memory rather than perceptual input (6, 8). These all reflect situations when cognitive operations cannot flourish based on environmental input alone, and suggest the DMN may reflect the process through which existing representations in memory guide cognition (8). The ability to guide cognition using preexisting representations allows more complex cognition to emerge in an efficient manner, explaining why the DMN is linked to complex forms of cognition that can seem effortless and automatic.

Finally, these studies highlight the importance of time in understanding the functions of transmodal cortex. The analysis by Vatansever et al. (2) demonstrates that transitions between the acquisition and application phases of the WCST are instantiated by a transition from higher FPN activity to a state of higher DMN activity. Since the information encoded during acquisition is used to guide behavior in the application phase, these opposing states reflect cognitive operations that are nested within the broader goal of performing the task. In the analysis by Vidaurre et al. (1), a similar hierarchical pattern emerges, although at a much coarser level. Within the transmodal metastate, states 6 and 8 (Fig. 1*B*) correspond to patterns of opposition between the DMN and other networks within transmodal cortex. The authors also make complimentary predictions for behavior, suggesting that even though these states may be anticorrelated at specific moments in time, they could be linked to overarching cognitive states or processes. Thus, a common theme emerging from both studies (1, 2) is that shifting patterns of dominance between the FPN and DMN may reflect the organization of cognition across a broad time frame. Perhaps the most important implication of this temporal perspective is that it allows the anticorrelation between the DMN and FPN to be reevaluated. Although both Vidaurre et al. (1) and Vatansever et al. (2) capture the anticorrelated nature of these two networks in their analyses, their results are consistent with the possibility that patterns of dominance between these two networks may reflect aspects of cognition that, at least on certain occasions, can collaborate in the service of a temporally extended goal. Future research, motivated by the methodological and conceptual advances made in these two studies, may help to further understand how the interactions between these large-scale networks of transmodal cortex contribute to cognition that extends over time.

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