Journal Club

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The Critical Role of the Hippocampus in Mind Wandering

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Review of McCormick et al.

The last decade has seen an increase in studies investigating the neural correlates of mind wandering. Many studies have implicated the default network (DN), particularly the medial temporal lobe (MTL) subsystem of the DN (DN_{MTL}), as a primary network activated when someone's mind is wandering (Christoff et al., 2009). The DN_{MTL} comprises the hippocampus, parahippocampal cortex, retrosplenial cortex, ventromedial prefrontal cortex, and the posterior inferior parietal lobe (Andrews-Hanna, 2012). Although the DN_{MTL} as a whole has been linked to mind wandering, more precise roles of its specific nodes have not yet been elucidated.

Consideration of the typical content of mind wandering suggests likely roles for specific brain areas. Mind wandering content often includes (but is not limited to) prospection, episodic and semantic memories, introspection, and fantasies (Stawarczyk et al., 2011; Andrews-Hanna et al., 2013). Different ranges of temporal directions (past, present, future) may be experienced, with variations in episodic nature and personal relevance (e.g., being reminded of a movie versus remembering that you went to see that movie with friends last year), and modality (e.g., thoughts that are primarily visual or verbal). Thus it is likely that the hippocampus, given its involvement in episodic and associative memory, helps to generate the content of mind wandering (Mills et al., 2018). Indeed, the generation of episodic, visual thoughts about the past or future relies on the hippocampus. For example, the hippocampus is critically involved in mental time travel and visual scene reconstruction (Hassabis et al., 2007; Schacter et al., 2007). Moreover, hippocampal damage impairs the ability to vividly recall past events (Lah and Miller, 2008), imagine the future (Kurczek et al., 2015), and mentally construct novel visual scenes (Hassabis et al., 2007). In addition, famous patients with MTL damage (H.M. and K.C.) were previously described as being stuck in a "permanent present-tense" or "permanent presence" (Tulving, 1985; Corkin, 2013).

If the hippocampus plays a critical role in the generation of mind wandering content, then people with hippocampal damage may be expected to mind wander less about past and future, episodic, visual events than healthy controls. To test this prediction, McCormick et al. (2018) studied mind wandering in six patients with bilateral hippocampal damage. The patients were shadowed over two days during which they were asked to report what was on their minds at 20 time points. For each thought, the researchers determined whether it was linked to ongoing perception, such as objects or sounds in the room. Mind wandering was defined as thoughts that were not tied to concurrent perceptions. Temporal range (past, present, future), representation type (whether thoughts were knowledge-based vs grounded in experience; henceforth: semantic vs episodic), self-relatedness, and form of thought (visual or verbal) were also noted.

The authors compared the frequency and content of mind wandering in patients to that in 12 control participants. Patients did not mind wander significantly more or less than healthy controls. However, their mind wandering was more often related to the present and less about the past than controls. Patients also reported more atemporal and hypothetical thinking. Thinking about the future was infrequent for both groups. Compared with controls, patients reported fewer visual and more verbal thoughts. Within-subject comparisons revealed that controls mostly reported visual scenes, whereas patients were more likely to report verbal thoughts compared with ones consisting of visual scenes or objects. In patients, thoughts were also more semantic than episodic, and more self-related than non-self-related.

The observation that hippocampal damage is related to more atemporal, semantic, and verbal mind wandering suggests that the hippocampus might indeed

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play a role in the generation of specific types of mind wandering content. Importantly, the simple probability of mind wandering remained completely unchanged across individuals with and without hippocampal damage, providing some initial empirical support for the idea that where, rather than whether, your thoughts "wander" may be determined by the hippocampus (Christoff et al., 2016).

The results from McCormick et al. (2018) shed light on how the DN_{MTL} might give rise to mind wandering. Evidence from single-cell recordings has shown that spontaneous memories are preceded by activation of hippocampal neurons that were active during encoding (Gelbard-Sagiv et al., 2008). Similarly, recent work found that the left and right hippocampi were active 2 s before the onset of a spontaneous thought (Ellamil et al., 2016). The findings by McCormick et al. (2018) suggest that this activity might be related to mental time travel and the construction of mental scenes that constitute the content of much of mind wandering.

A recent proposal suggests that the hippocampus may also generate the variability in content that we experience during mind wandering episodes (Christoff et al., 2016). This variability arises when the activation of one hippocampal-neocortical ensemble triggers the activation of another because they partially overlap. This auto-associative process is also known as pattern completion (Marr, 1971), and can lead to thoughts that are conceptually disconnected from the here and now (Christoff et al., 2016; Mills et al., 2018). Impairments in this process might explain why mind wandering in patients with hippocampal damage tends to be about the present and themselves, rather than about more (temporally or personally) distant events.

Along with the hippocampus, the ventromedial prefrontal cortex (vmPFC) is part of the DN_{MTL} subsystem. Interestingly, mind wandering in patients with vmPFC damage also tends to be less about the future and more about the present than healthy or patient controls with brain damage outside the vmPFC (mainly in the occipital cortex; Bertossi and Ciaramelli, 2016). One possible explanation for this similarity is that disrupting connectivity between the hippocampus and vmPFC biases mind wandering toward the present. Previous work has shown that the strength of functional connections between the hippocampus and vmPFC is related to the degree of mental time travel during mind wandering (Karapanagiotidis et al., 2017). The vmPFC might not be directly involved in the generation of content, but rather in other processes that underlie spontaneous cognition, such as those associated with the explicit awareness of the content of thought, known as meta-awareness (Christoff et al., 2009; McCaig et al., 2011). Indeed, in contrast to patients with hippocampal damage, patients with vmPFC damage report less mind wandering in general (Bertossi and Ciaramelli, 2016). Thus, given the vmPFC link to meta-awareness during mind wandering, one possible explanation for the lower rates of mind wandering reported by individuals with vmPFC damage is that they are simply not aware that their mind is wandering due to a lack of meta-awareness (Bertossi and Ciaramelli, 2016).

As McCormick et al. (2018) have shown, the role of the hippocampus in mind wandering concerns the content of mind wandering rather than its rate of occurrence. According to the dynamic framework of spontaneous thought (Christoff et al., 2016), thoughts can be constrained deliberately (e.g., thoughts that are driven by goal-directed processes) as well as automatically (e.g., thoughts that are drawn in a particular direction due to factors such as affective salience that are outside of deliberate control). Thoughts that are highly automatically constrained (e.g., worrying about something) are thought to arise from interactions between the core DN subsystem (consisting of anterior mPFC, posterior cingulate cortex, and posterior inferior parietal lobule) and the salience network, which feed into the frontoparietal control network and the DN_{MTL}. In contrast, thoughts that are deliberately constrained are driven by the frontoparietal control network, feeding into the salience networks and core DN subsystem. Mind wandering is predicted to arise when both types of constraints are relatively weak, so the mind can move about more freely. Indeed, a meta-analysis of studies of rapid-eye-movement sleep, during which most dreams occur, suggests that the DN_{MTL} is more strongly recruited when deliberate constraints on thoughts are relatively weak (such as during dreaming), perhaps giving rise to variability in content (Fox et al., 2013; Christoff et al., 2016).

An important question to consider is what happens to our experience when the DN_{MTL} is no longer there to guide less constrained thoughts? McCormick et al. (2018) have provided some critical insight into this question. In the absence of a functioning DN_{MTL}, thoughts that would normally be driven by the DN_{MTL} might become more constrained by sources of automatic (e.g., by salience) and deliberate (e.g., by goal-directedness) constraints instead. Indeed, examples from McCormick et al. (2018) are in line with this suggestion. Patients' thoughts like "I'm thinking that you are right-handed", "I wonder what this box with all these cables does. But I have no idea." are highly constrained in terms of salience compared with control participants' thoughts. Similarly, thoughts like "I wonder whether I should eat another grape" and "I'm trying to avoid getting depressed about [how relationships change]" are quite goal-directed.

Critically, this also touches upon the question what constitutes mind wandering. Although a definitive answer is beyond the scope of this paper, it is important to note that the definition of mind wandering as perceptually decoupled thought may not capture some of the key qualities of the phenomenon. Recent work has suggested that mind wandering thoughts may not only vary in to what extent they are perceptually decoupled and task-related, but also how freely the mind moves from one thought to the next (Mills et al., 2017). A more in-depth analysis of the content of thoughts and how they dynamically unfold over time may reveal qualitative differences in mind wandering that could shed light on how it arises in patients with damage in the DN_{MTL}. This in turn could inform theories about the critical role of the hippocampus and other DN subsystems that have been closely linked to mind wandering thus far.

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