COMMENTARY

Are the hippocampus and its network necessary for creativity?

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If neuroscientists who are not memory researchers were asked, "What does the hippocampus do?" they might answer that the hippocampus (HC) is important for memory, and perhaps they might specify that HC is critical for episodic memory (remembering personally experienced past events) but not for implicit (nonconscious) memory or for working memory (briefly maintaining information online). Although this view from the 1990s is still largely accepted, the way many memory researchers conceptualize HC has gradually changed during the last four decades. First, there is now abundant evidence that HC is involved not only in episodic memory but also in implicit memory and working memory (1). As a result, many researchers today think that HC is not a key region of a memory system but a component that mediates a specific cognitive operation, which can be recruited by tasks traditionally associated with different memory systems if the tasks require that specific operation (1, 2). Although the nature of this operation is a topic of active research, a popular hypothesis is that the main function of HC is to associate different kinds of information (3). Of course, no brain region can support a cognitive task by itself; a region must team up with other brain areas, and HC often collaborates with the functionally and structurally connected angular gyrus (AG) (4). A second important development in our conceptualization of HC function was brought by evidence that HC—in collaboration with AG and a subset of default network regions known as the *core network*—mediates not only remembering past events but also imagining future events (5). This second expansion of HC functions is still within the memory domain, because imagining future events consists mostly in recombining fragments from memories of the past (6). In contrast, the third extension of HC's "job description" has been beyond the memory domain, into territories such as language, empathy, problem-solving, decision-making, and some forms of creative cognition (1).

This extension of HC and its network into the creativity domain represents the historical and intellectual context of the study by Thakral et al. in PNAS (7). The study focuses on a particular form of creativity called *divergent thinking*, which refers to the ability to generate creative ideas by combining diverse kinds of information in novel ways (7), as when someone missing a hammer pushes a nail into a wall using an iron pan. In previous studies, Schacter's group found that, if participants are trained to recollect specific details from a recent experience (*episodic specificity induction* [ESI]), divergent thinking performance is enhanced, suggesting this form of creativity involves episodic memory (8). Also, this effect was associated with increased activity in HC, AG, and other core network regions, which are closely linked to episodic memory (8). Yet, functional MRI (fMRI) can only demonstrate that these brain regions are involved in divergent thinking, not that they are necessary for this ability. This is where the Thakral et al. study (7) provides its principal contribution. Using a form of noninvasive brain stimulation known as *repetitive transcranial magnetic stimulation* (rTMS), they disrupted the function of HC and other components of the core network. This disruption—which was confirmed with fMRI—impaired imagining future events and divergent thinking. This finding provides causal evidence that both tasks depend on HC and the core network.

Modulating HC with rTMS

In rTMS, a coil placed on the scalp delivers multiple magnetic pulses, which modulate the function of the cortical brain area underneath the coil as well as connected brain regions. Thakral et al. use a type of rTMS called *theta-burst stimulation* (TBS), in which magnetic pulses are applied in short bursts spaced at a theta frequency. This feature makes TBS ideal to modulate HC function, given the strong link between this region and the theta band (9). The effects of TBS can be excitatory or inhibitory, depending on several

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factors, and Thakral et al. use continuous TBS (cTBS) to disrupt the HC and the core network. Although the direct effects of TMS impact only a couple of square inches of cortex under the center of the coil, its indirect effects spread to structurally and/or functionally connected regions, which, in the case of AG, include HC and other core network areas (4).

Several rTMS studies have found that TMS to AG affects episodic memory. For example, there is evidence that detrimental rTMS to AG reduces confidence on memory recognition responses (10) and that enhancing rTMS to AG boosts associative memory (11, 12). These behavioral changes may reflect direct effects on AG, which has an important role in episodic memory retrieval in its own right (4), or indirect effects on HC and the core network. The rTMS effects can spread to distant regions, including the contralateral hemisphere, and can also trigger compensatory network responses (13). This is why it is optimal to measure and confirm TMS effects on the brain by following TMS application with functional neuroimaging, as Thakral et al. do (7). Using fMRI, they find that cTBS on AG attenuates functional connectivity between AG and HC and reduces activity in HC and other core network regions during both critical tasks investigated: future event imagery and divergent thinking.

Divergent Thinking Depends on HC

Future event imagery is investigated using the *episodic simulation task* (7). In each trial of this task, participants read a cue word (e.g., "brick"), imagine a near-future event associated with the word, and then rate the vividness of the generated image and the difficulty in generating it. In a previous study (14) in which the episodic simulation task was compared with a past-oriented version of the same task (e.g., remembering a past event associated with the word "brick"), both versions activated overlapping HC and core network regions, consistent with the idea that imagining the future consists in rearranging pieces of episodic memories (6). After scanning, participants in the Thakral et al. study provided details about the future events they generated in the scanner. Interestingly, cTBS reduced internal/episodic details (specific a particular time and place) but not external/nonepisodic (off-topic or commentary), consistent with the idea that the effect is mediated by the episodic component of the episodic simulation task. The second cognitive function disrupted by cTBS is divergent thinking, which was measured with the well-studied *alternate uses task*. In this task, participants are asked to generate alternative (but appropriate) uses for common objects (e.g., a brick), which independent raters subsequently score both quantitatively (number of uses, number of types of uses) and qualitatively (originality, level of detail). The key behavioral finding is that cTBS impairs both quantitative measures of divergent thinking (7).

This finding has implications for understanding the cognitive and neural mechanisms of creativity. As reviewed by Thakral et al. (7), although creativity has been traditionally associated with factual knowledge, also known as *semantic memory* (15), several pieces of evidence suggest that divergent thinking is also supported by episodic memory. For example, people sometimes retrieve episodic memories during divergent thinking, patients with episodic memory deficits tend to be impaired in divergent thinking, and divergent thinking activates HC and other core network regions that are strongly associated with episodic memory, etc. (15). Yet, this evidence is largely indirect and correlational. This is why the finding of Thakral et al. that episodic simulation and divergent thinking tasks are simultaneously impaired by the disruption of HC and core network functions—which is confirmed by fMRI—is particularly important. This finding provides previously unavailable evidence that episodic-related HC processes are not just involved in but, to a certain extent, necessary for divergent thinking.

This extension of HC and its network into the creativity domain represents the historical and intellectual context of the study by Thakral et al. in PNAS. The study focuses on a particular form of creativity called *divergent thinking*, which refers to the ability to generate creative ideas by combining diverse kinds of information in novel ways.

Beyond Divergent Thinking and HC

In addition to contributing this critical missing link, the results of Thakral et al. (7) are going to inspire future creativity research on the role of HC, AG, and other core network regions. Regarding HC, one interesting question is whether this region plays a role not only in divergent thinking but also in convergent thinking. Whereas divergent thinking tasks require the generation of multiple answers (e.g., alternative uses of a brick), convergent thinking tasks have one main solution. Convergent thinking tasks are assumed to depend almost exclusively on semantic memory, with no episodic memory component (15). As noted above, however, the function of HC is not limited to episodic memory; this region can be conceptualized as a processing component that mediates the operation of associating different kinds of information (3). Consistent with this idea, there is some evidence that HC is involved in the experience of insight, which refers to the sudden comprehension of a nonobvious problem that is accompanied by an AHA! experience. This is something that most scientists have experienced when unexpectedly finding the solution to a difficult problem. A few convergent thinking fMRI studies have found that HC activity increases with insight (16–18). This activity was attributed to the associative function of HC with the argument that insight occurs when multiple "puzzle pieces" finally fit together (18).

Another intriguing issue for future research is the role of AG in creativity (19). This component of the core network is strongly linked to episodic memory, but it also plays a major role in semantic memory (20). Again, the key contribution of AG might not be a particular memory system or form of memory but the specific cognitive operation this region mediates, which, in the case of AG, is a lively topic of research and debate (4). In sum, the Thakral et al. study (7) not only shows that HC and core network are critical for convergent thinking, but it also is likely to motivate further research on the role of these brain regions in this and other forms of creativity.

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