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COMMENTARY

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Mnemonic training contextualizes working memory with long-term memory representations: Commentary on Miller et al. (2022)

Jingyuan Ren[1] | **Boris N. Konrad**[1] | **Isabella C. Wagner**[2,3,4] | **Martin Dresler**[1]

[1]Donders Institute for Brain, Cognition and Behavior, Radboud University Medical Center, Nijmegen, The Netherlands

[2]Department of Cognition, Emotion, and Methods in Psychology, Faculty of Psychology, University of Vienna, Vienna, Austria

[3]Vienna Cognitive Science Hub, University of Vienna, Vienna, Austria

[4]Centre for Microbiology and Environmental Systems Science, University of Vienna, Vienna, Austria

Correspondence
Martin Dresler, Donders Institute for Brain, Cognition and Behavior, Radboud University Medical Center, 6525 EN Nijmegen, The Netherlands.
Email: martin.dresler@donders.ru.nl

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Human memory is not a single, homogenous storage space, but consists of different systems with different capacities, temporal dynamics and underlying neural mechanisms. Classical theories of memory differentiate between fast but transient working memory (WM) processes, and slow but longer-lasting memory structures for semantic and episodic information (Baddeley, 1992; Tulving, 1985).

A new study sheds light on the association between working memory and long-term memory: Miller et al. (2022) investigated influences of long-term training on neural representations in lateral prefrontal cortex during working memory engagement. Specifically, neural activity was repeatedly recorded with functional MRI in three participants extensively trained in a WM task and a sequence learning task, which both employed a unique set of complex fractal stimuli. The authors found that WM delay activity increased in the distributed representational structure of the lateral prefrontal cortex across several months of training. Also, item-level representation patterns in lateral prefrontal cortex became detectable during WM tasks, and lateral prefrontal cortex activity reflected sequence relationships from the sequence learning task. The study demonstrates that long-term training changed the distribution and representational structure of lateral prefrontal cortex function during WM engagement: Representations for specific stimuli and associations evolved over the course of training, indicating that the neural mechanisms for WM are influenced by prior experience stored in long-term memory. The findings thus suggest that behavioural increases in WM performance after extensive mnemonic training are based on representational formats in prefrontal cortex shared with long-term memory.

The study by Miller et al. is in line with other theoretical and empirical work emphasizing the interaction between working memory and long-term memory structures. The recently proposed WMEM model (Beukers et al., 2021) proposes an interactive account, combining existing theories of working memory (WM) and episodic memory (EM). The model aims to explain the phenomenon of *activity silent working memory*, that is, the phenomenon that attended items in working memory are actively maintained and can thus, for example, be

Abbreviations: EM, episodic memory; LTWM model, long-term working memory model; WM, working memory; WMEM model, working memory–episodic memory model.

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decoded with neuroimaging methods from ongoing brain activation, whereas unattended working memory items can be silently maintained, thus largely inaccessible to neuroimaging decoding strategies (Stokes, 2015). Rather than proposing working memory-specific, short-lasting synaptic weight changes made to the cortex, the WMEM model suggests that *activity silent working memory* might as well be mediated by longer-term traces within regular long-term memory structures. The model emphasizes the role of context representations maintained in working memory that allow episodic memory traces to inform performance on working memory tasks.

An important historical precursor of these different attempts to model long-term memory representations as integral parts of ongoing working memory processes is the *long-term working memory* (LTWM) model (Ericsson & Kintsch, 1995). The model—just as *skilled memory theory* as its own precursor (Chase & Ericsson, 1981)—aimed to explain memorization performances that exceed the normal range of working memory. The model proposes that during skilled working memory performance, information is encoded directly into a long-term memory context that can subsequently serve as a retrieval structure. Specific retrieval cues are explicitly associated with the encoded information, which can later trigger retrieval from long-term memory. These encoding and retrieval processes of long-term memory can be accelerated by training to such an extent that the memorizing speed approaches that of working memory. As a result, information active in working memory can trigger retrieval cues and retrieval structures, whereby the interconnected knowledge gets activated and is readily available for use in working memory.

Skilled memory theory and the LTWM model were inspired by earlier studies demonstrating that college students with a normal memory span equaling Miller's magical 7 ± 2 items expanded their working memory span to as many as 82 items after deliberate training (Ericsson et al., 1980). Today, these performances are widely exceeded in memory competitions such as the annual World Memory Championships, where memory athletes compete in different memorizing disciplines. For example, memory athletes regularly memorize hundreds of items with perfect accuracy in the classical number span task at a pace of 1 per second.

How do memory athletes manage to beat even the highest scores in classical laboratory-based working memory assessments by an order of magnitude? In a survey among the world's leading memory athletes, it was shown that they without a single exception attribute their memory skills to the use of mnemonic strategies such as the *method of loci* (Dresler & Konrad, 2013), that is, the ancient idea to associate to-be-memorized information with landmarks on well-known navigational routes also known as the *memory palace* (Figure 1). Recent research demonstrates that similar memory skills can be acquired also by naïve subjects with originally normal memory performance: Deliberate training in mnemonic strategies does not only behaviorally enhance memorizing skills considerably, but at the same time drives brain connectivity patterns towards those distinguishing memory champions from memory-normal controls (Dresler et al., 2017).

Mnemonic strategies like the method of loci represent prototypical retrieval structures as proposed in the LTWM model. Yet, mnemonic strategies are underutilized in psychology and cognitive neuroscience of memory and could in particular inform recent debates about the role of long-term memory structures in working memory processes. For example, in line with the WMEM conjecture that episodic context representations are information-theoretically cheap to maintain (Beukers et al., 2021), we recently observed that both memory champions and mnemonically trained novices exhibit very efficient neural coding when applying mnemonic strategies to memory tasks, with decreases in brain activation and neural representational similarity in the lateral prefrontal cortex (Wagner et al., 2021). Also Miller et al. (2022) in their new study observed a significant decrease in lateral prefrontal activity during WM encoding across training, suggesting similar enhancement of encoding efficiency.

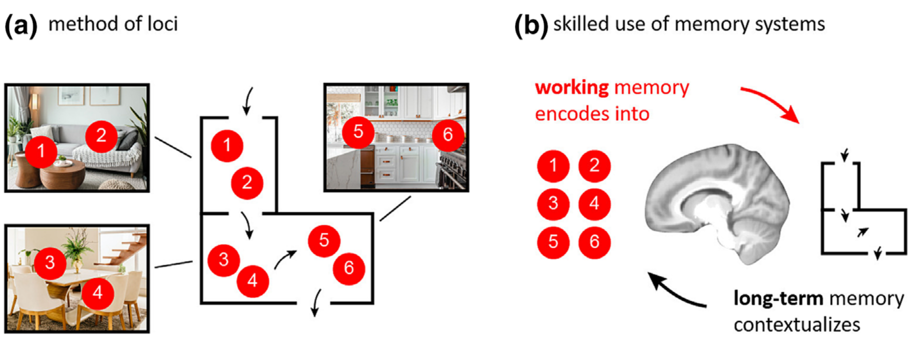

FIGURE 1 Working principles of mnemonic strategies. (a) The ancient *method of loci*—also known as the *memory palace*—associates to-be-memorized information with a pre-set sequence of landmarks on well-known navigational routes. (b) Skilled use of mnemonic strategies contextualizes current working memory content with representations from long-term memory.

Consistent with both the LTWM and WMEM models, but not with any account of only short-lasting changes underlying activity-silent working memory, memory athletes and mnemonically trained novices can not only memorize more information, but also contain it for longer than untrained control subjects (Wagner et al., 2021). Even if not intentionally utilized in experimental designs, the possibility of study material being encoded by mnemonic strategies should be considered carefully, as in our experience it can be difficult to exclude mnemonic strategies from (both long-term and working) memory tasks, and a considerable amount of the observed performance variance might actually be driven by habitual differences in the intuitive or explicit use of mnemonic strategies.

In summary, increasing evidence supports a role of long-term memory structures for working memory processes. Mnemonic strategies are prime examples for how working memory can be contextualized with long-term memory representations and are thus worthy of attention in all attempts to reconcile or disentangle the associations between working memory and long-term memory.

AUTHOR CONTRIBUTIONS

Conceptualization: Jingyuan Ren, Boris N. Konrad, Isabella C. Wagner, and Martin Dresler. *Supervision*: Boris N. Konrad, Isabella C. Wagner, and Martin Dresler. *Visualization*: Isabella C. Wagner and Martin Dresler. *Writing—original draft*: Jingyuan Ren and Martin Dresler. *Writing—review & editing*: Jingyuan Ren, Boris N. Konrad, Isabella C. Wagner, and Martin Dresler.

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The authors have nothing to report.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ORCID

Martin Dresler https://orcid.org/0000-0001-7441-3818

PEER REVIEW

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