

Volumen 42 | N° 3 | Diciembre 2024

Fecha de recepción: 21/06/2024 Fecha de aprobación: 16/10/2024 Fecha de publicación: 13/12/2024

https://doi.org/10.18537/RFCM. 42.03.08

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Artículo original

Original article

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Membrete bibliográfico

Peñaherrera MJ, Seade C, Vélez X. ¿Are the contents of working memory the activated part of longterm memory? A literature review on the activated long-term memory model. Rev. Fac. Cienc. Méd. Univ. Cuenca, 2024; 42(3):71-78. doi: 10.18537/RFCM.42.03.08

The contents of working memory as the activated component of long-term memory: a literature review on the activated long-term memory model

El contenido de la memoria de trabajo como la parte activada de la memoria a largo plazo: una revisión de la literatura sobre el modelo de memoria a largo plazo activada

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Abstract

Introduction: memory research traditionally views working memory (WM) and long-term memory (LTM) as separate processes, with WM holding and manipulating information temporarily, while LTM stores it indefinitely. Recent studies suggest these systems may be interconnected, with WM acting as an activated subset of LTM. Neuroscientific evidence, including fMRI studies, shows overlapping prefrontal activation during tasks involving both memory types. This review examines the theory of WM as an activated component of LTM, evaluating supporting and opposing evidence, and exploring the neural mechanisms underlying their interaction.

Objectives: this literature review aims to examine the relationship between working memory (WM) and long-term memory (LTM) in cognitive neuroscience. Specifically, it explores the theory that WM may be an activated component of LTM and evaluates the evidence supporting this idea. Additionally, it investigates recent findings suggesting that WM and LTM are not entirely separate systems but may be interconnected. The review also focuses on understanding the neural mechanisms, particularly prefrontal activation, that facilitate the interaction between these two memory systems.

Methodology: this review analyzes recent studies on the interaction between working memory (WM) and long-term memory (LTM), focusing on fMRI, neuropsychological research, and experimental tasks. It examines evidence for and against the activated LTM model, particularly regarding prefrontal brain activation during tasks involving both memory systems. Additionally, it explores cognitive theories on the integration of these systems.

Results: the literature review shows that working memory (WM) and longterm memory (LTM) are interconnected, with overlapping activation in prefrontal regions during tasks involving both. Functional MRI studies suggest that WM relies on LTM for retrieval, particularly when task complexity exceeds WM capacity. The prefrontal cortex plays a key role in both executive control and memory retrieval. However, there is evidence that WM and LTM may function separately in simpler tasks, indicating a need for further research to clarify their relationship. Overall, their interaction is complex and context-dependent. **Conclusion:** the findings suggest that working memory (WM) and long-term memory (LTM) are interconnected, with both sharing activation in the prefrontal cortex. This collaboration supports complex cognitive functions, though the activated LTM model is still debated. Future research should explore the mechanisms behind their interaction, particularly in executive control and attention.

Keywords: memory, memory, short term, memory long term.

Resumen

Introducción: la investigación sobre la memoria ha distinguido tradicionalmente la memoria de trabajo (WM) y la memoria a largo plazo (LTM) como procesos separados, siendo la WM responsable de retener y manipular información de forma temporal, mientras que la LTM la almacena indefinidamente. Sin embargo, estudios recientes sugieren que estos sistemas pueden estar interconectados, con la WM actuando como un subconjunto activado de la LTM. La evidencia neurocientífica, incluidos estudios de fMRI, muestra una activación superpuesta en la corteza prefrontal durante tareas que implican ambos tipos de memoria. Esta revisión examina la teoría de la WM como un componente activado de la LTM, evaluando la evidencia a favor y en contra, y explorando los mecanismos neuronales que subyacen a su interacción.

Objetivos: esta revisión de literatura tiene como objetivo examinar la relación entre la memoria de trabajo (WM) y la memoria a largo plazo (LTM) en la neurociencia cognitiva. Específicamente, explora la teoría de que la WM podría ser un componente activado de la LTM y evalúa la evidencia que apoya esta idea. Además, investiga hallazgos recientes que sugieren que la WM y la LTM no son sistemas completamente separados, sino que pueden estar interconectados. La revisión también se enfoca en entender los mecanismos neuronales, particularmente la activación prefrontal, que facilitan la interacción entre estos dos sistemas de memoria.

Metodología: esta revisión analiza estudios recientes sobre la interacción entre la memoria de trabajo (WM) y la memoria a largo plazo (LTM), centrándose en la fMRI, investigaciones neuropsicológicas y tareas experimentales. Examina la evidencia a favor y en contra del modelo de LTM activada, particularmente en relación con la activación de las regiones prefrontales durante tareas que involucran ambos sistemas de memoria. Además, explora teorías cognitivas sobre la integración de estos sistemas.

Resultados: la revisión de la literatura muestra que la memoria de trabajo (WM) y la memoria a largo plazo (LTM) están interconectadas, con una activación superpuesta en las regiones prefrontales durante las tareas que involucran ambos sistemas. Los estudios de fMRI sugieren que la WM depende de la LTM para la recuperación, especialmente cuando la complejidad de la tarea excede la capacidad de la WM. La corteza prefrontal juega un papel clave tanto en el control ejecutivo como en la recuperación de la memoria. Sin embargo, también hay evidencia de que la WM y la LTM pueden funcionar por separado en tareas más simples, lo que indica la necesidad de más investigaciones para aclarar su relación. En general, su interacción es compleja y depende del contexto.

Conclusión: los hallazgos sugieren que la memoria de trabajo (WM) y la memoria a largo plazo (LTM) están interconectadas, compartiendo ambas activaciones en la corteza prefrontal. Esta colaboración respalda funciones cognitivas complejas, aunque el modelo de LTM activada sigue siendo debatido. La investigación futura debería explorar los mecanismos detrás de su interacción, especialmente en el control ejecutivo y la atención.

Palabras clave: memoria, memoria a corto plazo, memoria a largo plazo.

Introduction

The relationship between Working Memory (WM) and Long-Term Memory (LTM) has been a topic of extensive research and debate in cognitive neuroscience. Over the years, several theories have emerged to explain the interaction between these two memory systems, with some proposing that WM is simply the activated portion of LTM, while others argue that they are distinct systems with separate functions. The "activated LTM model" suggests that WM is not an independent system but rather the activated state of LTM representations. This theory has been supported by evidence of overlapping brain activation during tasks that engage both WM and LTM, particularly in prefrontal and hippocampal regions. However, there are also significant critiques of this model, with some researchers arguing that the observed brain activations do not necessarily imply a shared system and that WM and LTM may operate through different processes.

This ongoing debate reflects broader questions about how memory is organized and functions in the brain. While some researchers maintain a clear distinction between WM and LTM, others propose that the two systems are more interconnected and mutually supportive than previously thought. In this context, the current work aims to explore the different views surrounding the activated LTM model, examining the evidence supporting and challenging this theory, and considering the implications for our understanding of human memory. By reviewing both opposing and reconciling perspectives, this work seeks to shed light on the complex relationship between WM and LTM and contribute to the ongoing conversation about how these memory systems interact within the brain.

Development

Memory research has traditionally categorized working memory (WM) and long-term memory (LTM) as distinct processes, where WM is responsible for the temporary retention (seconds to minutes) of a limited amount of information, and LTM for the longer retention (minutes or more) of data with a higher or potentially unlimited storage capacity^{1,2,3}. However, both memory systems contribute to the performance of a range of tasks, from simple to complex, in daily life and novel situations². Interestingly, the same prefrontal brain regions implicated in WM are also involved in supporting LTM³. These overlapping functions have sparked debate in the neuroscientific community about the relationship between WM and LTM, specifically whether WM represents an activated process of LTM⁴.

Working memory and long-term memory: distinct processes or interconnected systems?

One of the key arguments for the idea that working memory (WM) is an activated part of long-term memory (LTM) is the observation that WM capacity relies on retrieving information from LTM5. A study⁶ examined differences in accessibility to LTM (recall) by evaluating subjects with high and low WM capacity (determined by a z-score of three different span tasks). Participants were presented with a list of categorical words (six categories per list) in either a blocked format (category label presented first, followed by each word within the category) or a random format (without category labels or specific word order). Two recall conditions were considered: free recall, where participants were given two minutes to recall as many words as possible from the presented list, and cued recall, where a category label appeared on the screen, and participants had two minutes to recall words from that category.

After analyzing the data, researchers concluded that there was a significant difference in accessibility to LTM between high-and-low WM capacity participants. Those with high WM capacity recalled more words and categories from the list, as well as more words from specific categories. Both groups performed similarly when given cues, suggesting that low-WM capacity participants struggle to access cues using an appropriate retrieval strategy⁶. This evidence may help explain the association between WM deficits and learning difficulties, where LTM plays a crucial role⁷.

In this context, it has been concluded that WM load is reduced by LTM's role in managing and grouping the data entering WM into fewer units. Thus, WM operates actively with the support of LTM⁸. This aligns with interference memory phenomena, which explain why WM sometimes struggles when attempting to access LTM representations. Such interference can occur during recall, when similar memories compete, leading to difficulties in accurate remembering⁹.

Some pioneering researchers in the activated longterm memory (LTM) model theorized that working memory (WM) and LTM occur in the same neural structures, with WM representing the activated state of LTM^{10,11}. More recent evidence suggests a strong correlation between WM and LTM measures¹². A block-fMRI study compared prefrontal activation in right-handed adults during LTM and WM face-recognition tasks. The WM task involved a delayed-recognition task with no repetition of novel stimuli, where participants were asked to remember a face and then determine whether it matched a probe face presented after a delay. The LTM assessment involved intentional encoding and face recognition tasks with longer delays. Participants were asked to remember several faces and later confirm if a probe face was among the previously presented group.

To ensure consistency, researchers matched the temporal parameters of each task and counterbalanced the specific stimuli. The results revealed significant overlap in prefrontal activation during both WM and LTM trials. Specifically, the left posterior middle frontal gyrus and the right and left frontal gyri showed overlapping activation during the encoding phase of both tasks. During the retrieval phase, the right superior frontal gyrus, left anterior middle frontal gyrus, right and left inferior frontal gyri, and right and left posterior middle frontal gyri were activated. The authors concluded that WM and LTM share complementary functions and should not be considered distinct memory systems³.

Evidence and debates around the activated long-term memory model

It has been suggested that for performance on span tasks, both working memory (WM) and long-term memory (LTM) interact as if they were part of the same system¹³. When analyzing the processes required to complete a complex span task, three significant components of memory become relevant: processing (WM), storage (WM/LTM), and retrieval (LTM) of data⁵. In this context, some experts have described WM as the active component of LTM, with attention serving as its primary ally^{10,14}. This view is supported by evidence that complex-operation span tasks can only be completed if WM and LTM work together⁵. Given that the number of items that can be actively retained ranges from 1 to 4 (dispelling the previously accepted "magical number 7" theory)¹⁵, it seems unlikely that a person could retain four items while simultaneously performing additional information processing tasks (e.g., solving equations). Therefore, targets that cannot be actively maintained would be retrieved from LTM when needed (e.g., recall)^{10,14,5}.

A complementary view is Hebb's dual-trace mechanism, which proposes that a "cellular assembly" (interconnected neurons forming a network) supports both working memory (WM) and long-term memory (LTM), with WM being reinforced by reverberant activity (the activated state) of this cellular assembly¹⁶. According to this view, the WM store might be considered the temporarily activated portion of the LTM store^{17,4}, located in similar brain regions and supported by the hippocampus, which binds together targeted representations from other regions¹⁸.

Despite extensive study, the activated LTM model remains controversial and widely debated^{19,20,21}. One criticism of this model is based on two fallacies: 1) the reverse-inference fallacy, which assumes that if the prefrontal cortex shows activation, then WM or LTM are involved, depending on the task^{22,23}; and 2) the correlation fallacy, which concludes that if LTM activity is observed during WM retention tasks, then LTM representations are responsible for that²⁴. However, activation alone is insufficient to support the activated LTM model; it is necessary to establish the computational function behind the apparent interaction between WM and LTM. Until this is clarified, any explanation remains speculative^{24,25}. Additionally, when an LTM task is performed in a neuroimaging research setting, new stimuli must be processed, and instructions need to be retained to comply with the activity; this could explain the observed WM activation evidence¹⁹.

The classic notion that WM and LTM are separate stores and, therefore, functionally distinct^{26,27}, provides the foundation for arguments against the activated LTM model, based on the differential effects observed in certain tasks^{28,24}. For example, a blockfMRI study investigated whether selective activation for WM or LTM occurs in prefrontal regions. The study involved a within-subjects design with 28 right-handed adults, who completed six runs performing a two-back WM task (following the n-back paradigm) and an LTM task involving intentional memorization (encoding) and subsequent yes-no recognition (retrieval). For each LTM condition (encoding or retrieval), two types of stimuli (unfamiliar faces and familiar words) were used to account for task-type vs. material-type effects. Results showed that the bilateral dorsotemporal prefrontal cortex was activated during the WM task but not during the LTM task, regardless of condition (retrieval or encoding)²⁹. This evidence aligns with cases of patients presenting amnesia linked to hippocampal damage, showing LTM impairments but preserved WM30, and patients with left-inferior posterior-parietal lobe lesions, who exhibit WM damage but intact LTM function^{31,32}.

The LTM-WM-integrated-system paradigm has also been challenged by evidence suggesting that executive functions, and not only WM, are involved in LTM, as is the case with many other cognitive domains³³. This perspective also helps explain the overlapping activation of WM and LTM in the prefrontal cortex³. One alternative explanation for this

overlap is to consider the computational demands involved in even simple encode-retrieval tasks. For example, if a task requires remembering a short sequence of three digits, with one of the digits repeated (e.g., 1,3,1), it cannot be assumed that the mere activation of the digit representation in LTM would maintain the order of the two tokens of the repeated digit. Instead, this function should be attributed to an independent executive control domain, which, of course, includes WM²⁴. A complementary approach suggests that recency effects in LTM have different properties from those in short-term memory. Therefore, two memory components are needed to account for these recency effects: an episodic contextual system with changing context and an activation-based short-term memory buffer that drives the encoding of item-context associations³⁴.

Conclusions

A recent evolutionary neuroscience argument suggests that, in addition to the prefrontal and posterior parietal cortex, which are shared only by anthropoid primates (including humans), a specific lateral and rostral portion of the prefrontal cortex appears to be uniquely present in humans. These regions are responsible for specialized executive-control and decision-making abilities³⁵. Given that all vertebrate animals, from those exhibiting rudimentary learning (e.g., classical conditioning) to more sophisticated learning, seem to possess forms of long-term memory (LTM) and sensory-short-term memory^{36,37}, it is plausible that the brain regions specialized in executive control and working memory (WM) evolved as a separate system from LTM³⁶. As a result, interactions between WM and LTM are more likely to occur as a mechanism of executive control over LTM, rather than as an integrated system with WM acting as the activated section³³.

The different perspectives on the activated LTM model have been crucial in advancing our understanding of memory functions and its organization within the brain³⁸. Despite decades of extensive debate, some researchers continue to support^{10,15,39} and oppose^{24,19} the model, while others have produced evidence and theories that attempt to reconcile both views. For example, it has been proposed that working memory (WM) recruits long-term memory (LTM) representations only when beneficial⁴⁰, and that this interaction is closely tied to task complexity and attentional control. When a task is demanding, WM may seek support from LTM^{41,40}. This aligns with evidence suggesting that when the information to be learned exceeds WM capacity, task execution relies on LTM, even for brief retention intervals⁴². Some studies have further proposed that the interaction between WM and LTM is primarily observed in verbal memory, supporting language acquisition and development⁴³. This support system is crucial because the quality of new words' representation in WM plays a key role in consolidating a well-established phonological representation in LTM^{44,45}, and LTM phonological representations are essential for immediate recall, which also aids in the representation of new words⁴⁶.

In addition, many of the arguments for and against the activated LTM model share common implications, and these are often similar to those used by researchers who attempt to reconcile both perspectives⁴⁰. For example, the idea that WM and LTM must work together to perform a complex span task has been used as evidence in favor of the activated LTM model⁵, while a similar argument suggesting that executive functions (including WM) support LTM has been used to refute the model³³. This WM/LTM dissociation does not necessarily contradict the notion that each system is crucial to the functioning of the other; instead, the focus should be on how this interaction occurs. Therefore, it is worth considering whether the more reconciliatory approaches might offer a better understanding of human memory⁴⁷.

In conclusion, the growing trend in neuroscientific research to reconsider areas that were once viewed as distinct, and to explore brain functioning through networks, could represent a turning point in the ongoing debate over whether WM is merely the activated portion of LTM. For example, investigating the relationship between WM and LTM within the Multiple Demand brain network —strongly linked to a wide variety of cognitive tasks^{48,49} —could offer valuable insights into how these two memory systems interact and support complex cognitive processes.

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Contribution of the authors

All authors declare that they have contributed equally to the conception, design, analysis, and interpretation of the data.

Conflict of interest

No conflicts of interest.

Financing sources

The research was self-financed.

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Revista de la Facultad de Ciencias Médicas Universidad de Cuenca ISSN: impreso 1390-4450 digital 2661-6777

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