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Working memory forgetting: Bridging gaps between human and animal studies

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ABSTRACT

The causes of forgetting in working memory (WM) remain a source of debate in cognitive psychology, partly because it has always been challenging to probe the complex neural mechanisms that govern rapid cognitive processes in humans. In this review, we argue that neural, and more precisely animal models, provide valuable tools for exploring the precise mechanisms of WM forgetting. First, we discuss theoretical perspectives concerning WM forgetting in humans. Then, we present neuronal correlates of WM in animals, starting from the initial evidence of delay activity observed in the prefrontal cortex to the later synaptic theory of WM. In the third part, specific theories of WM are discussed, including the notion that silent versus non-silent activity is more consistent with the processes of refreshing and decay proposed in human cognitive models. The review concludes with an exploration of the relationship between long-term memory and WM, revealing connections between these two forms of memory through the long-term synaptic hypothesis, which suggests that long-term storage of interference can potentially disrupt WM.

In the 19th century, Ebbinghaus demonstrated that while the retention of recently acquired information tends to decrease rapidly over time, certain information can be retained for days, months, or even years (Ebbinghaus, 2013). This robust phenomenon, which has been documented many times since, has led psychologists to propose that memory can be divided into 1) a rapidly decaying 'primary' or short-term memory, and 2) a more stable 'secondary' long-term memory (James, 1890). The limitations of short-term memory have been observed in tasks known as immediate serial recall; tasks in which individuals are asked to recall series of digits, letters, or words immediately after their presentation. Through such experimental paradigms, it has been demonstrated that the maximum number of items an adult can maintain and immediately recall is about 7 plus or minus 2 (Miller, 1956), confirming that information indeed fades rapidly with time.

To highlight its dynamic nature, short-term memory was initially described as functioning as a "working memory", controlling the flow of information into and out of long-term memory, and playing a crucial role in action planning, learning, and cognition in general (Atkinson and Shiffrin, 1968). The term "working memory" gained widespread

recognition when Baddeley and Hitch (1974) introduced the first memory model, the 'multicomponent model', specifically dedicated to working memory (WM). Since then, WM has been generally defined as a limited-capacity system with a set of components that temporarily hold a limited amount of information in a state of heightened availability for use in ongoing information processing (Cowan, 1988).

All studies concur that WM is inherently limited. However, the factors limiting WM capacity have been a significant issue in cognitive psychology for decades. At least three main hypotheses have been proposed to account for this limitation in humans: decay, interference, and limited resources (Oberauer et al., 2016). Numerous experimental paradigms have been designed to test these hypotheses, but the results of these behavioral experiments have often been insufficient to conclusively refute any single hypothesis. For instance, Lewandowsky et al. (2010) observed lower recall performance when the level of interference, manipulated by the number of distractors and their novelty, was increased, leading the authors to conclude that forgetting primarily results from interference due to novelty encoding. Conversely, Plancher and Barrouillet (2013) observed no effect of the number of distractors or

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their novelty level on recall performance when attentional demands were controlled, suggesting that temporal decay is a more likely source of forgetting than novelty-based interference. From our perspective, the causes of forgetting in WM may continue to be sources of controversy, partly because it is challenging to study its neural mechanisms in detail in humans. Currently, sensitive techniques to explore these rapid cognitive processes in the human brain are still lacking. In contrast, animal models offer an advantage as they allow for the exploration of more precise neural mechanisms.

The aim of this review is to synthesize theoretical perspectives on cognitive mechanisms of WM in humans with neural mechanisms observed in animal models of WM, to assess whether these perspectives align. First, we will explore the principal causes of forgetting currently debated in human cognitive research. Second, we will examine the proposed mechanisms of WM in animals, particularly focusing on the delay activity model which may be underpinned by various cellular mechanisms, such as those related to the functions of action potentials (Fuster and Alexander, 1971; Goldman-Rakic, 1995; Kubota and Niki, 1971) or synaptic activity (Mongillo et al., 2008). We will conclude with a discussion on the recent long-term synaptic hypothesis, which suggests 1) that interferences can be stored in LTM and disrupt the storage of new information in WM and 2) that a mechanism can be established to erase these interferences. This final section will highlight the importance of considering the relationship between WM and long-term memory in explaining the mechanisms of forgetting.

1. Cognitive mechanisms of WM forgetting

The first hypothesis explaining limited WM capacity posits that forgetting occurs because WM representations decay over time, although this decay can be countered by maintenance mechanisms (Baddeley et al., 1975; Barrouillet et al., 2011; Cowan, 1999, 2012; Page and Norris, 1998; Ricker and Cowan, 2010; Towse and Hitch, 1995). As early as 1958, Brown proposed a theory of forgetting based on the premise that memory traces simply decay over time (see Ricker et al., 2014, for a historical overview of decay theories). Since then, various researchers have supported the idea that memory traces experience temporal decay in the short term (Baddeley et al., 1975; Barrouillet et al., 2011; Cowan, 1999, 2012; Page and Norris, 1998; Ricker and Cowan, 2010; Towse and Hitch, 1995). Among the most notable decay theories is the Time-Based Resource-Sharing (TBRS) model (Barrouillet et al., 2011; Barrouillet and Camos, 2014; Plancher and Barrouillet, 2019). This model postulates that processing and storage functions within WM compete for a single, shared resource, leading to a necessary trade-off between these two functions. The TBRS model is based on three main assumptions: First, both storage and processing require attentional resources; however, because this resource is limited, it must be shared between the two functions. Second, a central bottleneck constrains cognition so that only one elementary cognitive step can occur at a time (Pashler, 2016), necessitating that processing and maintenance activities occur sequentially. The third assumption is that WM traces are subject to temporal decay and interference as soon as attention is diverted. Thus, when attention is dedicated to processing, unattended memory traces decay; conversely, when attention is focused on maintenance, processing tasks must be delayed. To prevent memory loss, attention must frequently shift back to the maintenance/storage of memory traces for their restoration during brief pauses created by concurrent processing, and from storage back to processing when items need to be processed. This rapid toggling between processing and storage is managed through an executive loop that facilitates the construction, restoration, and transformation of WM representations. It is crucial to note that the role of attention is central to several models of WM, which conceive the attentional process of restoration as a covert retrieval (Cowan, 1992; McCabe, 2008; Unsworth and Engle, 2007), an attentional refreshing (Raye et al., 2007), a scanning of WM content (Vergauwe and Cowan, 2014, 2015), or a reconstruction of WM

representations (Barrouillet and Camos, 2014).

It is important to note that while the TBRS model acknowledges that interference can impact WM processing and maintenance, it does not view decay as the sole cause of forgetting. Instead, other models challenge the notion of decay and attribute forgetting primarily to interference (Lewandowsky et al., 2009; Nairne, 1990; Oberauer and Kliegl, 2006). According to the second hypothesis of forgetting, our ability to maintain multiple representations concurrently is limited because these representations can interfere with each other (Nairne, 1990; Oberauer and Kliegl, 2006; Saito and Miyake, 2004) or may be subject to interference from external distractors (Oberauer et al., 2012). These theories propose that forgetting arises from the reduced accessibility of these representations, rather than from their decay or loss. Consequently, these models also dismiss the necessity of a maintenance mechanism, arguing instead that memory traces do not decay. This view questions the causal role of rehearsal, as suggested by interference models (e.g., Lewandowsky and Oberauer, 2015).

One prominent interference model is the Serial Order in a Box-Complex Span (SOB-CS) model (Oberauer et al., 2012), which suggests that interference can originate from distractors encountered during intervening tasks, with the level of interference depending on the novelty of the distractors (novelty-gated encoding - Oberauer et al., 2012). Additionally, in interference models, similarity plays a critical role. The more features shared between the memorized items and the processed items, the poorer the recall performance (Lewandowsky et al., 2010b). There are at least two types of similarity to consider: First, the similarity among the items to be remembered, which influences phenomena such as the phonological similarity effect where increasing phonological resemblance among items worsens serial recall performance (Conrad and Hull, 1964), described as interference by feature overwriting (Oberauer et al., 2012). Second, the similarity between items processed during the delay period and those to be remembered plays a role. Memory disruption is significant when the distractors processed are from the same content domain as the memory items. This interference due to lack of distinctiveness is supported by findings that distractors from different stimulus categories (e.g., words vs. digits) cause less disruption than those from the same category (Oberauer et al., 2012). The articulatory suppression effect is another example of disruption of memory by processing in the same domain (Baddeley et al., 1984).

A third hypothesis explaining forgetting in WM suggests that it may stem from a limitation in cognitive resources (Case et al., 1982; Just and Carpenter, 1992; Ma et al., 2014). According to this view, forgetting occurs because the cognitive resources available, which are finite, must be divided among simultaneously held representations and ongoing processes. Specifically, a cognitive resource is a limited quantity that facilitates a cognitive function, such as maintaining or retrieving a representation in WM, with its effectiveness increasing as more of the resource is allocated to it. This resource can be conceptualized as either continuous or discrete. An example of discrete resources is illustrated by the "slot model" (Cowan et al., 2012), where resources are divided into discrete units and allocated across different tasks in parallel. Resource sharing involves prioritization, where focusing on one cognitive function or process happens at the detriment of others that require the same resource concurrently. It is important to note that these three theories—decay, interference, and resource limitation—are not necessarily mutually exclusive. For instance, the TBRS model integrates all three, positing that WM traces not only compete for a limited resource but also suffer from temporal decay and interfere with one another.

The causes of forgetting in WM thus remain a source of controversy in humans. However, animal models provide an opportunity to identify concrete constraints on WM that human-based verbal theories often leave unexplored. By using animal models, researchers can investigate specific neural mechanisms that underpin different facets of WM, offering valuable insights that could be compared against the predominant reasons for forgetting observed in human WM. Particularly, the neurophysiological approach allows for the measurement of neural

activity—whether spontaneous or induced—during the retention phase in memory tasks. This approach can specifically target and analyze the rehearsal or refreshing processes that many WM models in humans propose as crucial for memory retention (Baddeley, 2003; Barrouillet and Camos, 2014; Camos et al., 2018; Cowan, 1988; Johnson, 1992).

2. First evidence of neural correlates of WM: delay activity in the prefrontal cortex

The prefrontal cortex (PFC) has been historically linked with WM functions. Early research at the cellular level discovered neural correlates of WM within this region. Single-unit recordings from behaving monkeys revealed that during WM tasks, there was an increased frequency of action potentials sustained over the delay periods of delayed-response tasks lasting a second or longer (Funahashi et al., 1989; Fuster and Alexander, 1971; Goldman-Rakic, 1995; Kubota and Niki, 1971). This heightened neural activity, known as ‘delay activity’, is characterized by its ability to selectively represent the stimulus being held in WM, with neurons showing increased firing rates for relevant stimuli (Miller et al., 1996).

Initially, these findings suggested that delay activity represented a stable encoding of WM contents. However, further studies revealed that the firing rates of neurons exhibiting delay activity could fluctuate significantly during the waiting period before a cue that signals the end of a WM task trial, either increasing as the probe is anticipated or diminishing (Watanabe and Funahashi, 2014). This indicates that delay activity is not solely concerned with short-term storage of information but also with future utilization of this information (Warden and Miller, 2010). These studies complement the conception of these delay cells as devices involved not only in remembering the past, but also in preparing future behaviors based on the subject’s demand. Delay activity may thus alternatively code retrospectively for the stimulus seen before the delay, or prospectively for the action to carry on once the delay has elapsed. Research on spatial WM suggests that such prospective action or motor planning may be directly associated with PFC neurons’ delay activity as initially described in the literature (Lebedev et al., 2004). Conversely, retrospective sensory coding might involve the activity of neurons in posterior brain regions like the parietal cortex, the brain regions responsible for the perception of stimuli in the first place (Curtis, 2006).

3. Mechanisms behind delay activity - ‘cellular bistability’

Several electrophysiological and computational studies have focused on unraveling the mechanisms behind delay activity, particularly through models rooted in the biophysical characteristics of individual neurons (Sreenivasan and D’Esposito, 2019). These models explore how neurons can maintain a persistent, elevated firing rate following brief stimuli, a phenomenon known as bistability. Experimentally, bistability has been induced in hippocampal slices by activating muscarinic cholinergic receptors (Egorov et al., 2002; Navaroli et al., 2012). However, this form of cellular bistability, while insightful, does not fully represent the complex network dynamics that likely produce the content-selective delay activity essential for executing WM tasks.

Further computational models have delved into the roles of feedforward and recurrent cortical networks, suggesting that the collective firing within neuronal assemblies could be fundamental for sustaining information temporarily in WM (Diesmann et al., 1999). However, these models suggest that a very precise and noise-free temporal coding must be ensured in these networks to implement the delay activity, a condition that might not be met *in vivo* when a subject is confronted to real-life scenarios involving WM capacities. Nevertheless, these complex networks’ models take into consideration the fact that delay activity cells are not only found in the PFC but also in other brain areas (Fuster and Jervey, 1981).

4. Beyond the prefrontal cortex

Although WM was predominantly associated with the PFC, it is now known that the areas involved in WM processing cover a wider network including the parietal cortex, sensory cortex, hippocampus and subcortical structures (Quentin et al., 2019). In the monkey cortex, multiple electrophysiological studies have demonstrated that the duration of neuronal responses to visual stimuli progressively increases across brain regions, from low-level processing areas like V1 (primary visual cortex) to higher-level processing regions such as the inferotemporal cortex, parietal cortex, and frontal cortex. The prolonged activity observed in the PFC may be attributed to its high proportion of recurrent circuits compared to primary sensory cortices. This phenomenon, although not fully understood, likely contributes to the observed differences in the duration of WM representations between low-level and high-level processing cortical areas (van Kerkoerle et al., 2017).

The cortical hierarchy present in all mammals, but notably developed in primates, likely plays a role in defining different types of WM with increasing stability as information moves towards higher-level cortical areas, characterized by longer-lasting activity patterns. This cortical hierarchy is also associated with the significance of feedback connections from high-level processing cortical areas to low-level areas, which activate NMDA (N-methyl-D-aspartate) glutamate receptors more prominently than feedforward connections (from low-level to high-level areas) and engage more intrinsic recurrent circuits than feedforward connections (Lamme, 2001). Activation of these NMDA receptors tends to prolong synaptic activity compared to glutamatergic AMPA (α -amino-3-hydroxy-5-methyl-4-isoxazolepropionic acid) receptor activity and selectively enhances neuronal excitability.

5. Coordination of neural populations through synchronization of short-term synaptic activity?

The fact that a distributed network of neuronal populations in several cortical and subcortical areas can be activated during a WM task raises questions about how the activity of these neural populations is coordinated. One proposed mechanism for coordinating this information involves the formation of neuronal assemblies distributed across different brain areas, supported by local brain oscillations. Supporting this hypothesis, studies utilizing local field potential (LFP) recordings have demonstrated synchronization among prefrontal, parietal, and sensory cortical areas during WM tasks. In cortical areas, LFP recordings primarily reflect the combined synaptic responses of inhibitory and excitatory neurons (Teleńczuk et al., 2017).

While LFP recordings lack the cellular resolution of single-unit recordings (with LFP spanning several hundred microns versus tens of microns for unit recordings), they provide valuable insights into WM mechanisms. Unlike action potentials, synaptic responses endure for several milliseconds and are influenced by short-term (seconds to minutes) and long-term (hours to days) plasticity phenomena. Additionally, WM processes at the cellular level may operate covertly and be less metabolically demanding compared to sustained neuronal spiking. Collectively, these considerations suggest that short-term synaptic plasticity, particularly prominent in certain cortical areas like the PFC or the hippocampus, could support WM-dependent delay activity.

6. A synaptic theory of working memory

As mentioned earlier, the enhanced spiking activity often observed during the delay period of WM tasks is considered a neuronal correlate of WM. However, several electrophysiological studies have shown that this increase in delay activity is often very modest and irregular, waxing and waning, and sometimes disappearing completely during part of the delay period (Barak et al., 2010). Based on these observations and the assumption that maintaining information in a spiking form imposes a significant energetic cost on the organism due to the high metabolic cost

of action potentials, [Mongillo et al. \(2008\)](#) proposed the "Synaptic Theory of Working Memory." According to this theory, WM might not depend entirely on spiking activity but on short-term forms of synaptic plasticity. These authors tested their hypothesis with a model of a recurrent network of integrate-and-fire neurons whose synaptic transmission can be transiently facilitated by increasing levels of residual calcium at the presynaptic terminals of neurons coding for an item to be remembered in WM ([Katz and Miledi, 1968](#)).

It is well known that calcium ions (Ca^{2+}) play a crucial role in synaptic transmission (See [Fig. 1](#)). When an action potential reaches the presynaptic terminal, it triggers the opening of voltage-gated calcium channels. The opening of these channels allows Ca^{2+} to enter the presynaptic terminal from the extracellular fluid. The influx of Ca^{2+} inside the presynaptic terminal triggers the fusion of synaptic vesicles with the presynaptic membrane, releasing neurotransmitters into the synaptic cleft. Neurotransmitters can then bind to receptors on the postsynaptic neuron's membrane, initiating its response (e.g., depolarization). Once neurotransmitters are released, calcium needs to be cleared from the presynaptic terminal to reset the system for the next action potential. This involves the activity of calcium pumps and exchangers. The concept of "residual calcium" refers to the lingering presence of calcium ions in the presynaptic terminal after neurotransmitter release. Maintaining optimal calcium levels is crucial for proper synaptic function. Too much or too little calcium can impact synaptic transmission and, consequently, neural communication.

The residual calcium hypothesis in the context of WM is based on the fact that calcium cannot be completely buffered during elevated frequencies of presynaptic action potentials. This results in a progressive

increase in presynaptic calcium concentration, which tends to induce increased neurotransmitter release (i.e., decreased failure rate in transmission) such as glutamate ([Katz and Miledi, 1968](#)). Because the removal of residual calcium from presynaptic terminals is a relatively slow process ([Salin et al., 1996](#)), [Mongillo and colleagues \(2008\)](#) hypothesized that memory for this item can be transiently held for about 1 second by this short-term synaptic facilitation without any enhanced spiking activity. Thus, an increase in the frequency of action potentials modifies synaptic weights through short-term plasticity that preserves a memory of neuronal activity lasting hundreds of milliseconds. Indeed, their model shows that as long as synapses remain facilitated (due to the presence of residual calcium at presynaptic terminals), memory for the item can be reactivated at the end of the delay period by presenting a weak nonspecific excitatory input to the network. This reactivation is expressed as a short epoch of synchronized activity (or population spike) during which almost every neuron in the population fires a spike within an interval of about 20 ms.

Interestingly, this population spike (pop spike) may also occur spontaneously during the retention phase, refreshing the synaptic weights and potentially participating in the rehearsal process (postulated by [Baddeley, 2003](#)) or the attentional refreshing process, a domain-general mechanism relying on attention to keep mental representations active ([Barrouillet and Camos, 2014](#); [Camos et al., 2018](#); [Cowan, 2012](#); [Johnson, 1992](#)). These maintenance processes could help bridge the gap over longer delays and participate in the successful recall of information even after several seconds or minutes. However, without such reactivation, the synaptic changes in question would quickly recede, dissipating the functional coupling of the neural networks

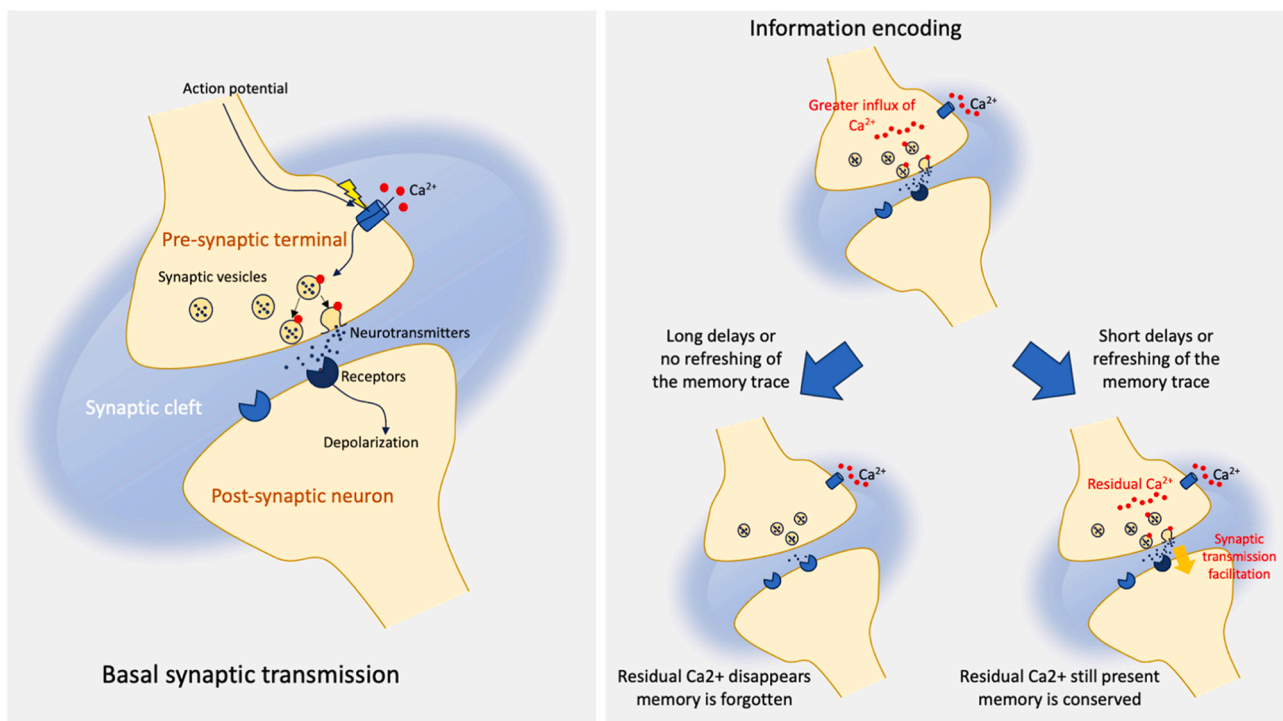


Fig. 1. (left) When an action potential reaches the presynaptic terminal of a neuron, it triggers the opening of voltage-gated calcium channels that allows Ca^{2+} to enter the presynaptic terminal. This Ca^{2+} influx in the presynaptic terminal triggers the migration and fusion of synaptic vesicles with the presynaptic membrane, releasing neurotransmitters into the synaptic cleft. Neurotransmitters can then bind to receptors localized on the membrane of the postsynaptic neuron, initiating their activation and the response of this neuron (e.g., depolarization). Once neurotransmitters have been released, calcium needs to be cleared from the presynaptic terminal to reset the system for the next action potential. This involves the activity of calcium pumps and exchangers (not represented here). (right) when WM information is encoded, it involves certain synapses and their activation. The concept of "residual calcium" refers to the lingering presence of calcium ions in the presynaptic terminal once the neurotransmitter has been released. The residual calcium hypothesis in the context of WM is based on the fact that in the presynaptic terminal, calcium cannot be completely buffered for elevated frequency (and short delays) of presynaptic action potentials. This results in a progressive increase in the presynaptic calcium concentration which tends to induce an increased release of neurotransmitters (i.e. due to a decrease of failure rate in transmission) the next time the same neurons/synapse is activated.

coding for the item held in WM and provoking its loss after a short time, an observation that could explain why WM has a short-term capacity. Mongillo and colleagues' model thus demonstrates that brief changes in synaptic strength could enable the rapid encoding of information that can be dynamically updated to maintain new information in WM. However, it is important to stress that, as long as the synaptically coupled neural networks that hold items in WM are not reactivated, they remain electrically silent (Stokes, 2015). The "Synaptic Theory of Working Memory" proposed by Mongillo and colleagues holds that the information encoded in these circuits would be maintained in WM similarly to how short-term or long-term memories are stored, and not by sustained action potential firing in these networks. The persistent spiking activity observed early during WM tasks (Goldman-Rakic, 1995) could thus be a byproduct of WM processing, reflecting more attentional processes than the temporary maintenance of information *per se* (Barak et al., 2010; Lewis-Peacock et al., 2012). WM and attention are two processes that are often intermingled. Attention ensures the selection of basic elements (or pieces of information), while WM ensures that the selected elements are actively maintained to be processed and assembled (Marchetti, 2014). At this stage, it is therefore possible to consider a dissociation between a passive maintenance mechanism relying on electrically silent mechanisms, as proposed in the "Synaptic Theory of Working Memory", and a more active maintenance requiring attention and relying on persistent spiking activity. Such a dissociation between passive and active maintenance mechanisms echoes works related to the potential difference existing with some forms of 'attended' working memories (in the immediate focus of attention) that are retained in conscious awareness, versus 'unattended' or nonconscious working memories that may operate through different cellular mechanisms.

7. Conscious versus unconscious WM

In 2017, Trübtschek and colleagues attempted to dissect the neural mechanisms of non-conscious WM (Trübtschek et al., 2017). In a spatial delayed-response task, participants were asked to report the location of a visual target presented very briefly (17 ms) after a delay of 2–4 seconds. However, due to the very short presentation of the stimulus, participants often reported not having seen the target. Surprisingly, their performance was above chance level, suggesting that they were able to correctly 'guess' the location of the stimulus. This result implies that although the participants reported not consciously perceiving or seeing the visual stimulus, their brains registered its location and could maintain it temporarily. As the authors also found no evidence that this prolonged blindsight could be explained by erroneous visibility reports or by the conscious maintenance of an early guess, they concluded that it reflects a genuine non-conscious storage of information in WM. The neural signatures of this non-conscious WM were compared to those observed when participants consciously processed information in WM and reported having 'seen' the items. They found that conscious WM, like conscious perception, was characterized by (1) sustained desynchronization in the alpha/beta band over frontal areas, which could reflect the interruption of an ongoing desynchronized beta default state by intermittent gamma bursts directly involved in encoding the memorized item (Lundqvist et al., 2011), and (2) slow decaying activity in occipital as well as temporo-occipital cortices that could maintain the target representation at least throughout the first part of the delay period. This second activity related to target 'decodability' seems to wax and wane afterwards, appearing and disappearing periodically during the rest of the delay. These findings demonstrate that maintenance in conscious WM gives rise to brain signatures similar to those observed during conscious perception and particularly conscious "ignition". According to the Global Neuronal Workspace Hypothesis (Mashour et al., 2020), "ignition" corresponds to the signal being broadcasted back and forth between brain areas, leading to an overall sudden increase in activation necessary for information to become consciously accessible. Trübtschek and colleagues' findings support the

view that conscious ignition could be the first step leading to the entry of information into conscious WM.

During non-conscious WM ('unseen trials'), however, such activity was not observed. The desynchronization in alpha/beta power observed for the 'seen' targets did not emerge during the 'unseen' trials, even when participants correctly guessed the location of the target after the delay (correct 'unseen' trials). Similarly, the slow decaying activity observed in posterior cortices during the first part of the delay period was not maintained afterward during the maintenance of unconscious ('unseen') WM trials (even correct ones). These results suggest that posterior sensory regions may initially encode seen and unseen memoranda in the same way, i.e., *via* slow decaying neural activity; however, in the case of unconscious WM, no intermittent activity reemerges during the remainder of the delay. Consistent with the idea of two states of maintenance in WM, one active and one passive, the Global Neuronal Workspace Hypothesis proposes that WM is conscious only when it is coded by global, highly distributed persistent neural firing (Mashour et al., 2020). This would occur during initial encoding, during the later refreshing stage, and when the memory item influences other mental processing steps. Additionally, according to this hypothesis, WM items that are outside the focus of attention would be coded by weaker persistent firing within local processors or by activity-silent synaptic mechanisms (Mongillo et al., 2008; Trübtschek et al., 2017). For the authors, items stored in memory stay unconscious until they are reinstated as globally distributed and sustained firing patterns. Christophel and colleagues (2018) seems to confirm this hypothesis by showing that the encoding of attended *versus* unattended contents involve different anatomical substrates. While the visual cortex would only maintain attended items, their study showed that intraparietal and frontal areas would represent both attended and unattended items. To explain these results, these authors thus propose that sensory cortices could maintain a high-resolution (and more precise) representation of the currently attended memory item, whereas the parietal cortex could have a low-resolution (and more abstract) representation of both attended and unattended items.

This perspective aligns with theories of WM in humans that delineate various activation states. Indeed, in several contemporary models of WM, such as Cowan's embedded-processes model (1988), Engle's model (Engle et al., 1999), and Oberauer's model (2002), WM is conceptualized as the temporary activation of specific portions of long-term memory. According to these models, the most actively accessed memory items (retrieved from long-term memory) are in the focus of attention. Items that are stored or refreshed in WM occupy the focus of attention, enabling them to be manipulated or updated. Additionally, a few other items may reside in an intermediate memory store with limited capacity, often referred to as 'short-term memory'. These items can easily enter the focus of attention and therefore into 'true' WM.

8. Unraveling unconscious WM

We can think of several daily examples during which WM can be maintained without conscious awareness and then recalled accurately when given an appropriate cue; for instance, when we forget our train of thought in a conversation but then recall it as soon as we are reminded of what was being said only seconds before. Rose and colleagues (2016) demonstrated that it is possible to artificially prompt this unconscious WM by delivering a single pulse of transcranial magnetic stimulation (TMS). In their experiments, participants were shown two visual items simultaneously on a computer screen. After a brief delay, they were cued to remember only one of these two items. Under these conditions, the cued visual object entered the focus of attention and was maintained in conscious (attended) WM to be tested after a few seconds delay, while the other object was not. Similar to Trübtschek et al. (2017), the authors found that the neural response associated with the object in conscious memory was sustained during this delay, whereas the neural response associated with the object held in unconscious, unattended

memory declined to baseline levels before the recall test. However, a single TMS pulse (applied 2–3 seconds after being cued to remember the object) was able to increase the baseline neural activity associated with the object in unattended memory. These results again suggest that latent, electrically silent, unattended memory could be maintained *via* mechanisms other than sustained elevated activity and that this 'activity-silent' WM (Stokes, 2015) could be reactivated by TMS.

However, firmly demonstrating the existence of such a silent phenomenon is challenging, especially in humans, precisely because it is... 'silent'. In contrast to animal models where evoked synaptic responses (Excitatory Post-Synaptic Potentials or EPSPs) can be recorded (Missaire et al., 2021), physiological techniques used in humans, such as EEG or fMRI, specifically monitor neuronal activity and not silent synaptic activity. New techniques therefore need to be developed to detect the presence of 'activity-silent' WM. To probe such hidden neural states in humans, Wolff et al., (2017) developed an approach to 'ping' the brain, akin to how sonar 'pings' the sea floor to reveal its hidden surface (see upper part of Fig. 3). These researchers hypothesized that if an electrically silent neural network representing information held in WM is formed and retained as long as the information is relevant, then the response of this network to an unrelated stimulus ('pinging' the network) should differ from the response if this silent network had not formed. In their study, participants were shown a screen displaying two objects that they were instructed to remember. After a short delay, a cue instructed the observer which object to remember for a subsequent test. This object would then be retained in attended WM, while the other

object would either be forgotten (experiment #1) or retained in unattended nonconscious memory to be recalled later (experiment #2). The results of the study (also see Barbosa et al., 2020; Douglas Fields, 2022) demonstrated that EEG activity increased after cueing the participant to remember the object. This EEG activity corresponding to the cued object was sustained until the recall test. However, the activity corresponding to the forgotten object (experiment #1) or the object to be recalled later (and thus maintained in unattended memory - experiment #2) slowly returned to baseline after 500 ms (see Fig. 2 upper left).

These results, reminiscent of those from Trübtschek and colleagues (2017 – see Fig. 2 upper right), support the hypothesis that different mechanisms sustain unattended and attended working memories, with persistent neural activity associated with attended memories but not with unattended ones. The researchers then employed a third unrelated visual stimulus to 'ping' the system and reveal the synaptic plastic changes that had occurred in the neural network theoretically recording the item stored in WM (see Fig. 3). This 'pinging' boosted neural activity for the object in attended memory, but to a much lesser extent for the object held in unattended memory as long as this object remained in the background (experiment #2), and not at all for the forgotten object (experiment #1). Conversely, when cued to remember the second object (only in experiment #2), 'pinging' boosted neural activity for this second object now in attended memory, but not for the first object that became irrelevant. The authors concluded that, unlike attended WM, unattended but still relevant for future use (experiment #2) WM is stored by synaptic plastic changes forming dynamically coupled,

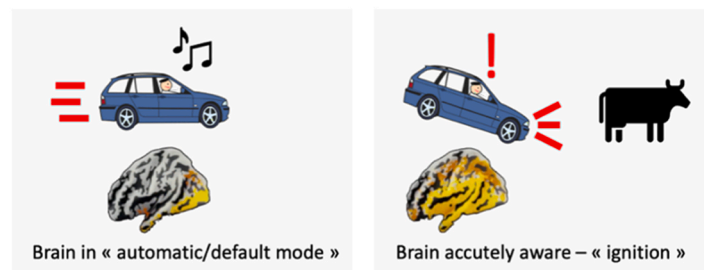
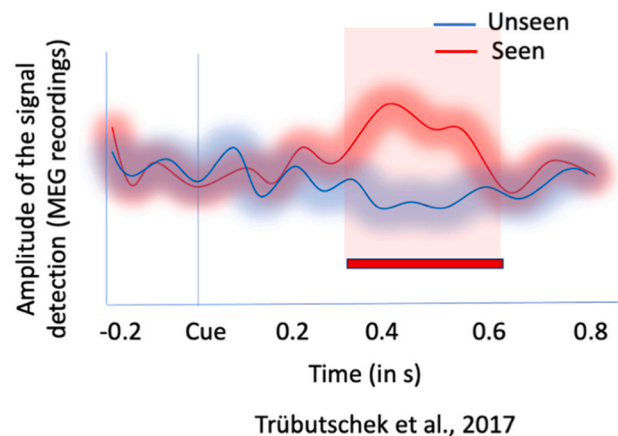
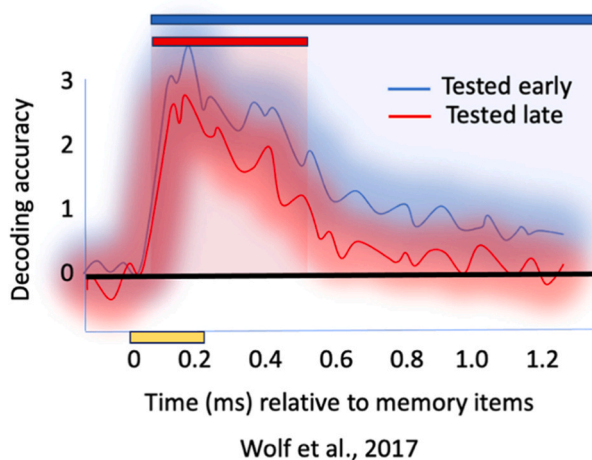


Fig. 2. Conscious versus unconscious WM: (upper left) schematic representation of the results obtained by Wolf and colleagues (2017) after presentation of visual items (yellow bar) later tested for their recall in a WM task. Results of experiment #2 indicated that the decodability of the early-tested item (blue) is prolonged as compared to the one of the late-tested item (red). (upper right) this result is reminiscent of those obtained by Trübtschek and colleagues (2017) showing that persistent neural activity is associated with attended (seen – red) memories, but not with unattended (unseen – blue) memories. The figure represents the schematic sequence of brain activations (-200 – 800 ms) evoked by consciously perceiving the target in a WM task. (lower) Decodability' thus seems to wax and wane during a delay typically used in WM task. Maintenance in conscious WM gives rise to brain signatures similar to the ones observed during conscious perception and in particular conscious "ignition". According to the Global Neuronal Workspace Hypothesis (Mashour et al., 2020), "ignition" corresponds to the signal being broadcasted back and forth between brain areas, leading to an overall sudden increase in activation that has to occur in the brain for information to become consciously accessible like it is the case when a driver (driving in a semi-automatic mode - left) needs to be acutely aware of its surroundings when an expected event (represented by the cow - right) occurs on the road ahead.

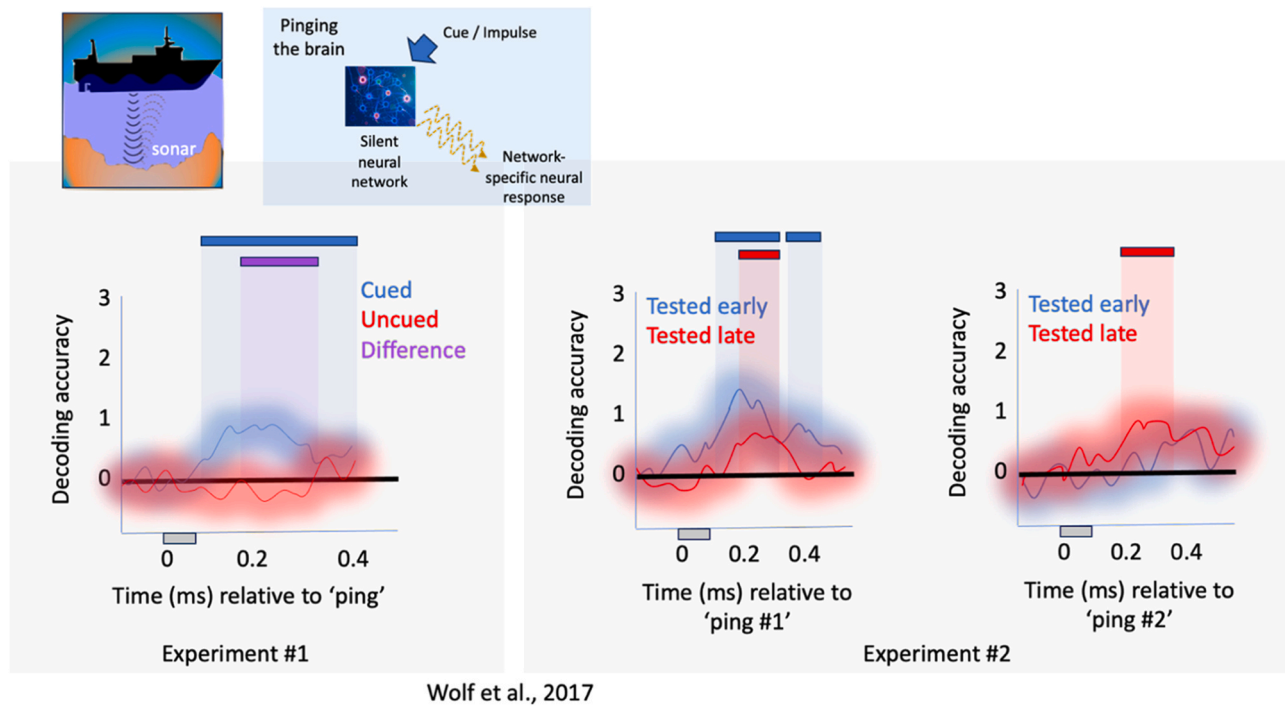


Fig. 3. To uncover the existence of silent-activity WM mechanisms, Wolf and colleagues (2017) developed an approach to ‘ping’ the brain, like a sonar ‘pings’ the sea floor to reveal its hidden surface (upper left). The researchers used a visual stimulus (unrelated to the ones that participants needed to remember – see Fig. 2) to reveal the changes that have occurred in the neural network that theoretically recorded the items stored in WM. This ‘pinging’ boosted neural activity (decodability) for the object in attended memory (blue), but 1) much less for the object held in unattended memory (red) as long as this object remained in the background (experiment #2 – lower central), and 2) not at all for the forgotten object (experiment #1 – lower left - red). Conversely, when cued to remember the second object (only in experiment #2), ‘pinging’ boosted neural activity for this second object (red) now in attended memory, but not the first object (blue) that became irrelevant (lower right).

electrically silent neural networks that can nevertheless be ‘pinged’, without the requirement for ongoing increases in neural activity (Mongillo et al., 2008).

However, recently, a new interpretation of these results has been proposed. Barbosa and colleagues (2021) reexamined Wolff and colleagues’ data (2017) and found that the neural response to the object in unattended memory could be sustained for the entire duration of the delay. Instead of simply monitoring EEG voltage, Barbosa and colleagues analyzed the power of the alpha band displayed in the EEG activity. They found that sustained alpha power code tracks both the attended and unattended items that remain relevant for future behavior (in experiment #2), but not the unattended item that is to be forgotten (in experiment #1). This result shows that WM contents can be maintained in an electrically active neural code as long as they remain relevant for future use, even for items that are not in the immediate attentional focus. However, while attended memories would be decodable both in alpha power and voltage traces, unattended but still relevant memories could be kept in analogous but weaker alpha neural signals. Through their reanalysis of Wolff and colleagues’ datasets, Barbosa and colleagues (2021) thus show that WM “reactivations” by visual pinging, considered by Wolff and colleagues to be the prime evidence of an activity-silent WM (Wolff et al., 2017), occur in the presence of active, and therefore not silent, ongoing WM representations during the delay period. Interestingly, Barbosa et al. (2021) also reexamined Rose’s data (2016) and found that single-pulse TMS increases across-trial EEG variability, in contrast to the reduction observed upon visual pinging (Wolff et al.’s study, 2017). Such increase in across-trial variability supports the interpretation of TMS (but not pinging) EEG reactivations as signals recovered from activity-silent traces. In fact, Stokes and colleagues (2020) caution against a direct equivalence between functional states in WM (attended/‘active’ versus unattended/‘latent’ WM) and their corresponding neural states (sustained/persistent

versus silent activity). Stokes and colleagues add that “the key theoretical constraint is that active and latent WMs should be maintained via qualitatively distinct neural states”. Within this context, the Barbosa and colleagues’ re-analyses (Barbosa et al., 2021) thus reinforce the idea that interpreting an absence of apparent decoding activity as evidence for storage in silent traces can be misleading, ‘because null results might result from weak signals in insufficiently powered analyses’. However, the reverse is also true: an absence of evidence of activity-silent WM does not mean that activity-silent WM does not exist at all.

9. Activity-silent or not silent WM

In fact, the entire issue concerning activity-based and activity-silent WM arises from the perception that they are viewed as exclusive alternatives. Because one is often considered the opposite of the other, it is challenging to imagine that they can coexist (Barbosa et al., 2020). Interestingly, however, modeling studies (Kilpatrick, 2018) have argued that serial biases could represent a behavioral situation where these two mechanisms could interact. Serial biases in spatial WM correspond to small but systematic shifts of memory reports toward nearby locations memorized during previous trials, revealing lingering representations of past memories that play the role of proactive interference. Using a behavioral paradigm generating such serial biases, Barbosa and colleagues (2020) demonstrated that the interaction between activity-based and activity-silent WM can be observed in the PFC of both monkey and human subjects during the inter-trial interval (ITI), a time period believed to ‘reset’ the content of WM so that information from past trials does not interfere with newly formed information required for the ongoing trial (Roberts and Dale, 1981). The authors showed that while a substantial fraction of PFC neurons exhibited stable and persistent delay activity during the intra-trial mnemonic delay (the delay period typically studied in WM), the firing rates of these neurons

displayed another type of strong but fluctuating dynamics during the ITI. Once the test recall of trial n was completed (mid-ITI), PFC neurons were no longer tuned to the previous stimulus held in WM (decoding accuracy was not different from chance), suggesting that the encoding of this stimulus from trial n had disappeared from neural activity. However, this stimulus information reappeared just before the presentation of the new stimulus in trial $n + 1$ (end of the ITI), consistent with models predicting that activity encoding a previous target location can persist into the subsequent trial (Papadimitriou et al., 2016). The authors demonstrated that during the mid-ITI period, stimulus information could not be decoded before reappearing at the end of the ITI, indicating that the memory for the previous stimulus could be momentarily held through activity-silent mechanisms before being reactivated to bias behavioral performance in the subsequent trial. They further reasoned that if such activity-silent synaptic mechanisms affect a group of interconnected neurons, it would enhance synchronicity but not the rate of firing of these neurons, a phenomenon convincingly demonstrated in their study (Barbosa et al., 2020). Importantly, they also found that the reactivation observed at the end of the ITI correlated with the strength of serial biases in both monkeys and humans. Additionally, single-pulse transcranial magnetic stimulation (TMS) applied to the human PFC between successive trials enhanced serial biases, demonstrating the causal role of these PFC reactivations in influencing WM performance.

Interestingly, in the investigations conducted by Rose et al. (2016) and Wolff et al. (2017), no explicit mention was made regarding the participants' awareness of the reactivated memories, despite the observable resurgence of activity-silent working memory (WM) items to a decoding accuracy surpassing chance levels subsequent to transcranial magnetic stimulation (TMS) or the ping/impulse stimulus. This indicates that pinging activity-silent WM does not induce conscious awareness of the reactivated memories, suggesting that these memories remain subliminal within the documented instances thus far. The subliminal nature of reactivated memories is consistent with studies showing above-chance behavioral memory performance for items retained over WM delay periods in the absence of conscious awareness (e.g. Trübutschek et al., 2017). This also aligns with the fact that more than just silent brain activity is required to bring memories into consciousness, memories remaining conscious only when it is coded by global, highly distributed persistent neural firing (Mashour et al., 2020). In future studies, it would be interesting to investigate the relationship more systematically between the neural state of memories and their level of consciousness by explicitly inquire participants about their subjective perception of the awareness regarding the reactivated memories.

To summarize, WM remains conscious only when it is encoded by global, highly distributed persistent neural firing (Mashour et al., 2020), such as during initial encoding of an item or during the retention delay when the memory is refreshed (Trübutschek et al., 2017). WM items that are outside the focus of attention may be encoded by weaker persistent firing (in the alpha band - Barbosa et al., 2020) or by activity-silent synaptic mechanisms (Mongillo et al., 2008; Wolff et al., 2017; Douglas Fields, 2022). These activity-silent synaptic traces remain unconscious until they are reinstated as globally distributed and sustained firing activity. Importantly, this perspective suggests that activity-silent WM differs from activity-based WM in that only the latter can be mentally transformed and manipulated, whereas activity-silent states merely passively store previously encoded information (Barbosa et al., 2020).

A more recent study by Trübutschek and colleagues (Trübutschek et al., 2019) indirectly addresses this issue. They demonstrated that when information in WM needs to be manipulated, an active form of WM is reinstated, accompanied by classical signatures of conscious processing, whereas this reinstatement does not occur when the information is merely stored. Their findings challenge the concept of genuine non-conscious WM and suggest that activity-silent states primarily support passive forms of short-term memory, rather than WM *per se*. WM is distinguished from short-term memory by specific attributes such as

executive control for filtering out distractors, limited capacity, and internal manipulation of information (Wang, 2021). However, this does not imply that activity-silent states do not impact WM. Indeed, as mentioned earlier, indirectly decodable neural states such as short-term synaptic facilitation (Mongillo et al., 2008) may interact with persistent delay-dependent spiking activity to influence the behavioral performance of subjects in various WM tasks (Barbosa et al., 2020). Short-term synaptic facilitation could represent the trace of information encoded during the trial immediately preceding the ongoing WM trial, contributing to proactive interference on newly encoded information needed for accurate retrieval in the current WM task. Interestingly, recent research has shown that long-term synaptic plasticity can also generate interference that subsequently impacts WM performance negatively.

10. Long-term synaptic modifications and memory processes

Among the various forms of synaptic modifications, long-term synaptic plasticity has been the most extensively studied. Based on the assumption that sustained modifications of synaptic strength leave a lasting trace of initially encoded information in the brain (the engram - Tonegawa et al., 2015), it is commonly believed that long-term memory relies on Long-Term Potentiation (LTP). LTP corresponds to a prolonged increase in synaptic transmission initially observed in the rabbit's hippocampus after applying trains of electric stimulations intended to mimic learning processes (Bliss and Lømo, 1973). Several animal studies have demonstrated that pharmacologically (Morris, 2003) or genetically (Kandel Eric, 2000) altering the molecular cascade involved in LTP similarly affects long-term memory consolidation. However, demonstrating that learning leads to long-term synaptic modifications in the brain has proven more challenging (Takeuchi et al., 2014). The most direct method to detect such changes is to record evoked responses (field EPSPs) in freely moving animals, particularly in the hippocampus, after training these animals in tasks involving long-term memory consolidation. Nonetheless, the detection of these LTP-like changes has been limited to animals trained in highly stressful and intense procedures involving, for example, the application of several electric foot-shocks (to create a long-term memory of this traumatic experience - Whitlock et al., 2006). Recently, we demonstrated that training rats in a more ecological behavioral paradigm also induces LTP in the dentate gyrus of the hippocampus (Missaire et al., 2021). Rats were trained to retrieve food pellets in an 8-arm radial maze over two days (see Fig. 4 A). In a task designed to assess long-term memory (also called Reference Memory or RM), rats had to learn the consistent location of food rewards always placed in the same position within the maze. We found that one day of training in this long-term memory task led to a sustained increase in synaptic responses recorded in the dentate gyrus (Fig. 4B bottom left). This LTP-like phenomenon was observed 9 hours after training, confirming that the storage of information in long-term memory is a gradual process requiring consolidation time. This LTP was also correlated with improved performance when rats were subsequently tested in the task 24 hours after the initial day of training (Missaire et al., 2021), suggesting that this LTP is directly involved in the consolidation of long-term memory.

However, it is also known that the hippocampus is not the final resting place of the engram, and several studies have shown that this structure plays a temporary, not permanent, role in memory storage (Winocur et al., 2010). Once consolidated, a memory trace is believed to be permanently stored in the neocortex, not the hippocampus. Consistent with this hypothesis, we observed that once the rats had mastered the long-term memory task (displaying 100 % correct responses after two days of training), a prolonged (long-term) decrease (or depression) in synaptic responses replaced the LTP observed in the dentate gyrus the day before (Fig. 4B bottom right). This Long-Term Synaptic Depression (LTD) is often associated with the removal or forgetting of information (Malleret et al., 2010; Nicholls et al., 2008) and could be involved in resetting the hippocampus once a memory has been stored elsewhere. As

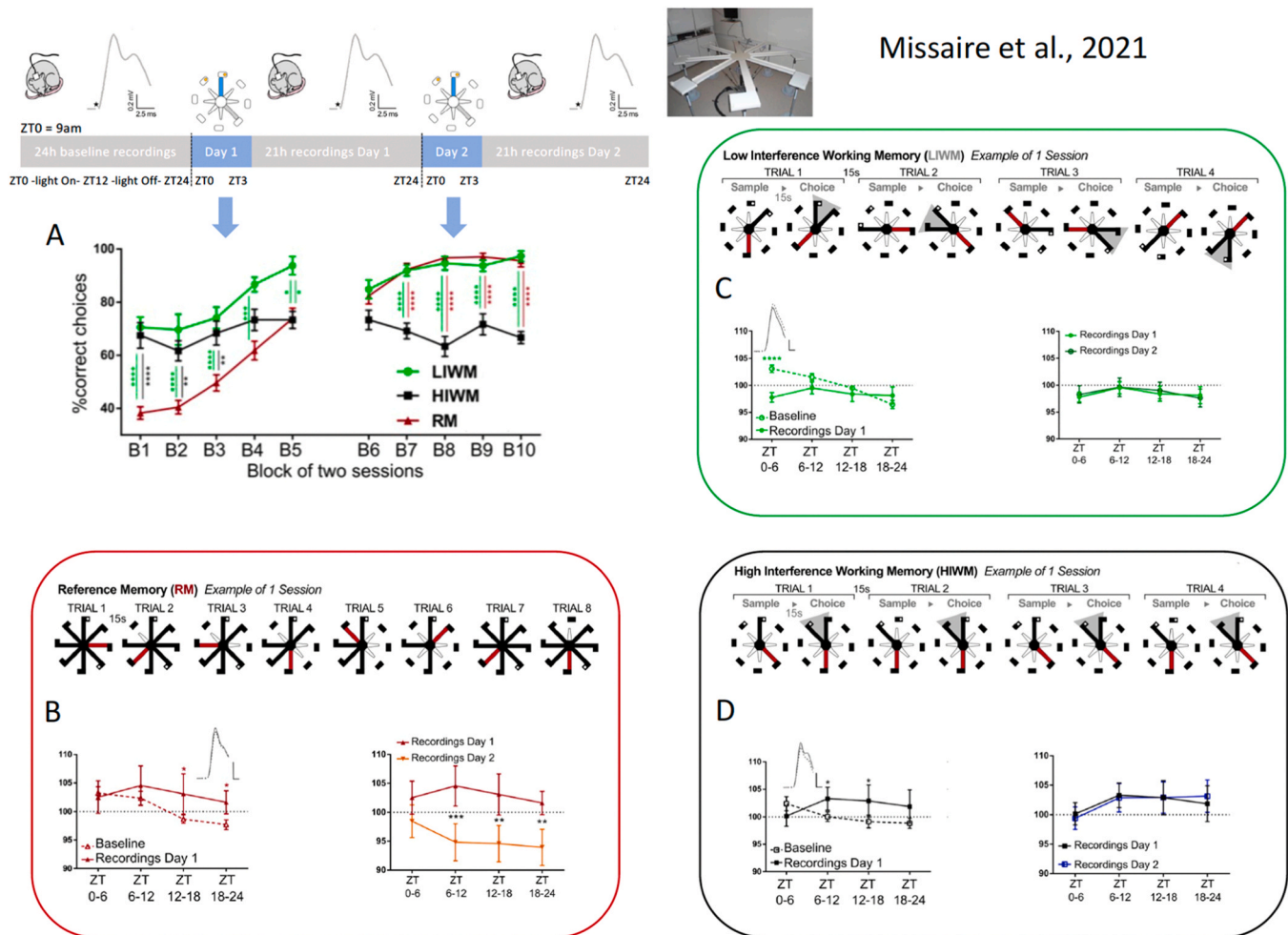


Fig. 4. adapted from Missaire et al., (2021). (A) Behavioral performance (percentage of correct choices) of groups of rats trained over 2 days in 3 different radial maze tasks, averaged by blocks of 2 sessions (an example for 1 session in each task can be seen in the top parts of B, C and D). Performance in the long-term (or Reference) memory (RM) group is lower than in the WM groups at the beginning of training, but rats rapidly learn the rule and improve their performance across the 2 days of training, reaching a level of performance equivalent to the one observed in LIWM rats on Day 2. Performance in the LIWM group is higher than in HIWM and improves between the 2 training days, whereas HIWM performance stagnates at a lower level across the 2 days of training. (B-D) Direct within-period comparison of the fEPSP slope (normalized to the averaged slope on 24 h of Baseline) between Baseline and the first day post-training (bottom left), and between the first and the second day post-training (bottom right). The bottom left analyses revealed 1) a significant early synaptic depression after LIWM training ((C) during the first 3 h post-training—ZT3–6) compared with the same period in Baseline, 2) a significant late synaptic potentiation in the HIWM group starting 3 h and ending 15 h post-training ((D) ZT6–12–ZT12–18), and 3) a significant late synaptic potentiation in the RM group starting 9 h and ending 21 h post-training ((B) ZT12–18–ZT18–24). The bottom left analyses revealed that the significant late synaptic potentiation after the first day of RM training (B bottom left) is followed by a synaptic depression after the second day of training (B bottom right). ZT = Zeitgeber Time.

mentioned earlier, this "reset" is a distinctive attribute of WM that must be cleared once retrieved, ensuring that previously stored information does not interfere (proactive interference) with the storage and recall of newer information. Hippocampal LTD could participate in this memory reset (and the forgetting of proactive interference) and benefit rats trained in WM tasks. To test this hypothesis, we also trained rats in delayed-non-match-to-place (DNMTP) tasks in the radial maze (Missaire et al., 2021). DNMTP tasks are traditionally used to test WM in rodents, as well as in humans and non-human primates. The task is simple: during a 'sample phase', the subject must temporarily store information—in the rat's case, the location of an arm where it can obtain a food reward—to retrieve this information during a subsequent 'choice phase' seconds later (delay), avoiding the original location (non-match) and instead choosing a new, adjacent arm of the maze in order to retrieve a second food reward. Our study employed two DNMTP WM tasks (Fig. 4C-D): a low interference (LIWM) and a high interference (HIWM) WM task involving variable levels of proactive interference (Missaire et al., 2017). The only difference between the LIWM and HIWM tasks was the

pairs of arms used for each trial in the radial maze during a single session. In the LIWM task, different pairs of arms were used for each trial of a given session (four trials with four different pairs of arms, resulting in the visit of all eight maze arms during a session), whereas in the HIWM task, the same pair of arms was used for all trials. The HIWM task was therefore more repetitive than the LIWM task, with similar information stored in WM, increasing the level of proactive interference (Underwood, 1957) and impairing the performance of rats trained in this task compared to those in the LIWM task, as consistently shown in past studies (Fraize et al., 2016, 2017; Joseph et al., 2015; Missaire et al., 2017). These two types of WM training induced distinct changes in synaptic transmission in the dentate gyrus. Optimal processing of interference in rats trained in the LIWM task (rapidly achieving 100 % correct choices) triggered synaptic depression immediately after training (Fig. 4 C bottom left), lasting for three hours (LTD-like), which, considering the role of LTD in forgetting, could act as a mechanism for interference erasure. In contrast to the observed LTD after LIWM training, synaptic transmission was potentiated 3–15 hours after HIWM

training (resembling the delayed potentiation seen after long-term memory training - see Fig. 4D bottom left). This LTP-like phenomenon was negatively correlated with rat performance on the second training day, suggesting that this potentiation was detrimental and maladaptive to information processing in WM. While the LTD observed after LIWM training facilitated forgetting of previously stored information (interference), the LTP-like phenomenon after HIWM training could prevent such forgetting and instead contribute to the consolidation of past information (Day 1), interfering with WM processing on the subsequent training day (Day 2 - see Fig. 4 A). This result highlights an interesting aspect: WM can be influenced by memories stored the previous day (and therefore stored in long-term memory).

11. Relationship between long-term memory and working memory

Over the years, researchers studying human memory have increasingly focused on understanding the relationship between WM and LTM. This relationship can be explored in three main ways: first, by investigating how information is maintained in WM depending on whether it is present in LTM or not; second, by studying how WM mechanisms influence the formation of LTM traces; and third, by examining how interference "stored" in LTM affects WM. It is important to note that WM experiments with humans typically use familiar material (e.g., letters, words, images). Therefore, most WM tasks do not require participants to learn new information, as the presented items are already stored in their LTM. Previous research has explored how pre-existing content in LTM affects WM maintenance. For instance, a study investigated whether the beneficial effect of a maintenance mechanism—refreshing—on long-term retention could be generalized to pseudowords (Loaiza et al., 2014). Results demonstrated that the benefit was observed with words (preexisting in LTM) but not with pseudowords (not preexisting in LTM). To explain these findings, the authors suggested that preexisting semantic representations may be necessary for optimal refreshing. Similarly, other studies suggest that refreshing cannot effectively maintain unconventional characters (Ricker and Cowan, 2010), character fonts (Vergauwe et al., 2014), or unfamiliar melodies (Nees et al., 2017). These results align with recent theoretical models of WM. The covert retrieval model (Loaiza et al., 2014; McCabe, 2008) proposes that refreshing involves covert retrieval of semantically meaningful memoranda from LTM, enhancing context-content associations and facilitating recall. The revised version of the TBRS model developed in humans mentioned earlier makes similar predictions by including a re-integration mechanism, enabling degraded traces to be reconstructed from the content of LTM (Barrouillet and Camos, 2014). Together, this literature suggests that novel material lacking representation in LTM may not benefit from refreshing. However, findings from other studies indicate that WM can maintain information on material not already present in LTM (Labaronne et al., 2023a; Loaiza and Camos, 2018), challenging the notion that WM necessarily relies on LTM representations. On the other hand, when examining the relationship between WM and LTM, researchers can explore how WM contributes to the construction of LTM traces. Several studies suggest that maintenance in WM, particularly refreshing (as opposed to verbal rehearsal), influences both WM and LTM performance (Camos and Portrat, 2014; Jarjat et al., 2018, 2020; Johnson et al., 2002; Loaiza and McCabe, 2013). For example, using a complex span task, researchers observed that providing more opportunities for maintaining information in WM (by increasing the delay between items to be processed) enhances LTM (Jarjat et al., 2018, 2020; Labaronne et al., 2023b). However, these results have not been consistently replicated, as the effect of cognitive load is robust when recall is immediate but not when it is delayed (Labaronne et al., 2023a; Loaiza et al., 2023). These inconsistent findings suggest a complex relationship between WM and LTM.

Another example of LTM items influencing WM performance is found in the effects of proactive interference. For example, Oberauer and Awh

(2022) investigated whether WM performance exhibited signs of proactive interference, a hallmark of retrieval from LTM. They observed proactive interference for set sizes larger than four but not for smaller set sizes, indicating that LTM may support performance when WM capacity is exceeded. Crucially, they found that performance with small set sizes remained resistant to proactive interference even after prolonged interruptions by a distractor task. They interpreted these results as evidence that memories resistant to proactive interference imply activity-silent storage in WM. Given the presumption that WM items coded by activity-silent mechanisms are those outside the focus of attention, it indirectly suggests that WM items are immune to interference once they are no longer in attentional focus. Consistent with this, Bae and Luck (2017) demonstrated through serial dependence biases that WM representations interact with each other depending on attentional priority. In experiments where participants memorized teardrop orientations, similar orientations repelled each other, while dissimilar orientations were attracted to each other. Importantly, when one item received higher attentional priority through a cue, the representation of the high-priority item was minimally affected by the orientation of the low-priority item. However, the representation of the low-priority item was significantly influenced by the orientation of the high-priority item, showing that WM representations influence each other depending on attention. Investigating the relationship between activity-silent WM traces and attention in the future should be important to provide a better understanding of interference phenomena in WM.

As previously observed, prior decoding studies have shown that information can be moved back and forth between active and activity-silent states within a single trial of a WM task (Rose et al., 2016; Wolff et al., 2017). Going further, Bae and Luck (2019) investigated whether reactivation from an activity-silent representation is possible for information from previous trials that is no longer task-relevant, which could explain phenomena like proactive interference or priming. In two experiments where participants once again had to memorize teardrop orientations, they found that the previous-trial orientation could be decoded from the current-trial EEG, indicating that the current-trial stimulus reactivated the representation of the previous-trial orientation. Their findings demonstrate that processing a new stimulus can trigger the reactivation of a previous experience even when that experience is no longer relevant to the task. More generally, they suggest that investigating neuronal mechanisms of WM may provide potential mechanisms for classic cognitive phenomena such as proactive interference, serial dependence, and other priming effects. Additionally, such studies enable testing of cognitive theories of WM. At first glance, the results of Bae and Luck (2017), (2019) seem to contradict cognitive theories of WM assuming that, in addition to actively maintaining information, WM also involves actively deleting information that is no longer relevant (Lewis-Peacock et al., 2018; Oberauer, 2009; 2018). Particularly in the SOB-CS model (Oberauer et al., 2012), it is proposed that interference is reduced in WM thanks to a removal mechanism that eliminates distractors encoded in WM, interfering with memory traces (Oberauer and Lewandowsky, 2014). However, a large number of experiments have shown that such a mechanism is unlikely (Dagry et al., 2017; Dagry and Barrouillet, 2017; Barrouillet et al., 2017; Barrouillet et al., 2012; Plancher and Barrouillet, 2013), by showing for instance a strong priming effect from distractors (Dagry and Barrouillet, 2017) or a good memory for distractors at delayed recall (Dagry et al., 2017). More recently, Rhilinger, Xu, and Rose (2023) tested the active-deletion hypothesis using orientations and a double-retrocue paradigm similar to that used by Rose et al. (2016) to examine repulsion and attraction effects of competing memory items. They reasoned that if irrelevant items are actively deleted, bias should be largest on recall 1 (because the uncued item is still potentially relevant on the trial) than on recall 2 (because it is no longer relevant on the trial). However, contrary to the active-deletion hypothesis, they found that no-longer-relevant items exerted the strongest bias on participants' recall. The results of Rhilinger et al. (2023) align with those of Bae and Luck (2017) but also of Missaire

and colleagues (rats' study), suggesting that irrelevant information is not removed from WM but, on the contrary, could be consolidated through long-term synaptic plasticity (Missaire et al., 2021).

There is an ongoing debate regarding whether WM and LTM represent distinct memory systems or if there exists a single memory system responsible for both short- and long-term storage (for a current view on this debate, see, for instance, Cowan, 2019; Norris, 2017). One prominent theory supporting the latter perspective is the Embedded-Processes Model (Cowan, 1999, 2019). According to this model, short-term memory results from a combination of information held in the focus of attention, the content of activated LTM (a subset of LTM readily available), and rapid learning of specific aspects of presented information (e.g., serial positions of list items) into activated LTM usable in the trial. Some theories propose that when attention shifts away from items to be maintained, returning them to the focus of attention involves retrieval from LTM (Atkinson and Shiffrin, 1968; Cowan, 1999; McCabe, 2008; Unsworth and Engle, 2007). These items, no longer in WM but possibly (or not) in LTM, might be related to the latent activity-silent memory traces mentioned earlier concerning non-conscious WM.

Traditionally, in humans (similarly to animal models), both cognitive and neural models of WM have suggested that information is retained in WM, either in capacity-limited, modality-specific buffers (visuospatial, phonological; Baddeley and Hitch, 1974), or in activated states of varying accessibility levels (Cowan, 1999; Oberauer, 2002), *via* sustained, elevated levels of neuronal activity. However, recent suggestions propose that information could be maintained in WM through activity-silent mechanisms in sensorimotor cortex regions (Rose, 2020; Trübtschek et al., 2017); and the synaptic theory of WM can explain that holding information in WM does not always require sustained activity (Mongillo et al., 2008). During a delay, a stimulus could be maintained by temporarily strengthening synaptic weights between neurons, without elevated neural firing. As previously mentioned, Rose and colleagues provided evidence for this phenomenon (2016); using brain decoding methods with simultaneous non-invasive brain stimulation, they transiently reactivated passively maintained (latent) WMs by recovering memory-specific patterns of neural activity, which influenced memory performance. These short-term plasticity mechanisms would differ from LTP mechanisms involving protein synthesis-dependent growth of new synapses that may underlie LTM representation (Mongillo et al., 2008). However, latent WM might be better conceptualized as LTM (Chao et al., 2023; Rose, 2020). This view aligns with the covert retrieval described by McCabe (2008). According to McCabe, inter-leaved distraction during complex WM span moves memory items out of the focus of attention and necessitates retrieving them from LTM. This could explain why memory might improve after complex span tasks compared to simple span tasks. Nonetheless, this view conflicts with evidence suggesting that items not previously in LTM can be maintained in WM (e.g., Labaronne et al., 2023a). It might be that LTM retrieval processes and associated neural substrates are involved in short-term retention of information in some situations but not all, consistent with the Dynamic Processing Model of WM (Rose, 2020; Chao et al., 2023). Using a retro-cued paradigm where a retrospective cue directs participants to prioritize maintenance of one or more items in WM over others initially encoded and maintained in WM, Chao et al. (2023) observed that while retro-cueing significantly affects WM performance, it does not interact with or systematically affect subsequent LTM performance. According to the authors, these dissociations between WM and LTM suggest that maintaining and reactivating an item outside the focus of attention does not involve LTM retrieval processes. Overall, inconsistencies in results when studying the relationship between WM and LTM suggest that maintenance in WM might sometimes be achieved *via* active, dynamic, recoded representations in frontoparietal cortex, or *via* latent representations in sensorimotor cortex involving efficient synaptic plasticity mechanisms. The Dynamic Processing Model of WM posits that the latter case might be especially relevant in situations involving minimal interference.

In conclusion, the causes of forgetting in WM remain a subject of ongoing debate within the scientific community, primarily due to the challenges associated with investigating the intricate neural mechanisms underlying these rapid cognitive processes in humans. While current limitations of sensitive techniques for detailed exploration in the human brain contribute to the complexity of this inquiry, animal models provide valuable tools for delving into more precise neural mechanisms, offering insights that may complement our understanding of WM in humans. By navigating between human cognitive processes and findings from animal models, this review contributes to a holistic understanding of WM and lays the groundwork for future research aimed at unraveling the intricate neural underpinnings of forgetting in WM. This review article sought to bridge theoretical perspectives on WM cognitive mechanisms in humans with the neural mechanisms delineated in animal models. Initially, we addressed the contested causes of forgetting in human WM. Subsequently, we delved into the proposed mechanisms of WM in animals, with a particular focus on the delay activity model. We observed that conscious representation of WM appears to be closely tied to global, highly distributed persistent neural firing, aligning with observations during the initial encoding of an item and the retention delay when memory is refreshed. Conversely, items falling outside the focus of attention may be coded by weaker persistent firing or activity-silent synaptic mechanisms, which remain unconscious until reinstated as globally distributed and sustained firing activity. If the delay is too long, items would be lost, consistent with the WM decay hypothesis. The discussion continued with the exploration of a recent hypothesis—the long-term synaptic hypothesis—which posits that interferences in WM may be stored in LTM, consequently disrupting WM storage. Conversely, a mechanism may exist to erase these interferences. This final section underscored the emerging connections between WM and long-term memory, providing a nuanced perspective on the interplay between transient cognitive processes and more enduring memory systems.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the revision of this work the authors used ChatGPT in order to improve the writing of the manuscript. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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