

**Dynamic aspects of visual working memory storage; toward a complete account of representational changes in visual working memory over time.**

Femke R. A. M. Ruijs

Utrecht University  
Writing assignment  
Neuroscience & Cognition Masters Program  
Supervised by: Dr. Surya Gayet  
02-02-2024

**Table of contents:**

|  |       |
|--|-------|
| Abstract _____   | p. 3  |
| Introduction _____   | p. 4  |
| Intrinsic characteristics of visual working memory storage _____   | p. 7  |
| Effects of external factors on working memory storage _____        | p. 10 |
| Effects of internal factors on working memory representation _____ | p. 12 |
| Brief overview and speculation _____                               | p. 18 |
| References _____   | p. 25 |

## Abstract

Working memory (WM) is a dynamic and flexible storage system. It needs to constantly adapt to maintain and optimize WM storage in the face of interference and changing internal behavioral goals. Yet current research often focusses on analyzing WM as a stable entity. Here, WM representations are analyzed over an entire maintenance period. Furthermore, participants are often asked to perform a task about a few simple stimuli while looking at a grey screen. While this setup can provide answers about *where* information is stored and *what* might happen if one internal or external factor is added, it leaves out the *when*. This is problematic when dealing with a dynamic entity as WM, as representations can change or adapt over time. It could lead to null-results, as shifts in representation add noise to a block-analysis. Moreover, it does not provide a clear account of what WM does over time and how different mechanisms are employed to sustain human behavior.

In this review, current findings about dynamic WM mechanisms are discussed. We discuss intrinsic characteristics of WM storage and the effects of external and internal factors on WM representations. This includes dynamic shifting, neural drift, visual interference and attentional and behavioral goals. Additionally, some theories about the role of the early visual cortex in WM and possible activity-silent codes are discussed. We find that WM is highly dynamic, as it is constantly adapting and modulating neural representations of visual stimuli in the EVC in response to interference. We also find that WM can change representational formats depending on attentional demand to optimize maintenance of multiple items without having them interfere. To understand *when* these changes precisely happen, fMRI studies could benefit from temporal generalization methods. Here, a timeseries is analyzed and compared over multiple time intervals. Future studies could employ this analysis method, as well as combining intermixed and blocked experiment designs to isolate strategic and responsive WM adaptations. Finally, WM research could benefit from more complex research paradigms, where multiple tasks and/or interference methods are used with more complex stimuli. This would increase the ecological validity of WM studies, and help understand how WM adapts in our stimulus-rich environment.

Through this new dynamic focus on WM storage, we could understand more about this complex system that supports our daily functioning.

## Introduction

When looking both ways before crossing a street, you might not think twice about how you get a clear mental picture of the current traffic situation. You simply review the mental picture and decide whether to cross or not. However, the processes that underlie this visual picturing of previously seen environmental content are quite complex. Visual information needs to be memorized, retained, and integrated with new information, before providing a complete overview image which can then guide behavior. The system that underlies these processes is visual working memory (VWM). Visual working memory is a sophisticated and essential storage system that supports the active retention and manipulation of visual information in preparation or support of an upcoming task. More specifically, it supports these processes in the absence of the original sensory input of the item stored in memory.

In the previous example, one reviews and integrates visual information and then decides based on this information. However, VWM supports behavior and decision making in many more scenarios. For example, when you need to go to work, but need to find your keys before you leave. Here, the image of your keys need to be pulled from memory, maintained and compared to the outside world (Chen & Zelinski, 2006). Thus, the mental image of your keys needs to be steady in the face of changing visual input as you scan your surroundings for a match. Here, the mental image of your keys is actively stored in visual working memory and represented through neural activity.

Within this latter example, there are many possibilities of internal and external factors interfering and adapting how the visual information needs to be stored. For example, there is a constant stream of visual information entering the brain. The mnemonic representation of your keys need to be stable in the face of these external factors. Additionally, someone could ask you a question while you are searching. You would need to put the mnemonic representation on hold while still being able to access it later.

Though visual working memory is constantly used in internally and externally-rich environments, VWM research does not reflect this. Current working memory studies typically have a participant memorize one or more stimuli while they are fixating a uniform gray background screen, and then analyze the entire (event-free) retention period as a block, collapsing across all timepoints of the retention interval. This poses multiple problems. First, the experiment setup and stimuli used do not reflect the situations and stimuli for which VWM is used in the outside world. Second, analyzing the whole retention period as a block removes the possibility of understanding how VWM retention changes over time. Third, focusing on one single task/interference negates the possibility of discovering how multiple

internal and external factors affect visual working memory processes. While these studies provides an estimate of *where* and *how* VWM items are stored, it leaves out *when* and *how* these representations might have changed over time.

This lack of insight not only leaves questions about the *when* unanswered, but can also lead to *how* and *where* questions to not be answered fully. Since, if representations change forms and/or locations over time, but data is analyzed over an entire retention block, these shifts will be left undiscovered. Additionally, if representations change over time, it is possible that decoding models used to decode information from VWM might be looking for the wrong patterns, resulting in null-results.

Thus, visual working memory needs to be robust in the face of internal and external factors. Additionally, it needs to be optimally adapted to these factors. For example, when a task goal changes, the VWM representation needs to be aligned with this new task demand. However, current research does not accurately reflect this dynamic flexibility of VWM in both experiment setup and analysis. A more dynamic research approach is necessary to fully understand if, when, and how dynamic changes in visual working memory occur.

In this review, I will discuss currently available findings which provide insight into how WM representations might change over time. This will provide a theoretic framework for dynamic WM storage which can guide further research into this topic.

For this purpose, three distinct aspects of (dynamic) visual working memory storage will be addressed. First, intrinsic dynamic characteristics of visual working memory storage will be discussed. This encompasses all representational changes that occur naturally in VWM over time, such as introduced noise, neural drift, or general VWM processes that affect how and where visual information is stored over time. Second, the effect of external factors on VWM representations will be discussed. This includes factors such as distractors, visual interference, or other externally imposed events that might affect VWM. Third, internal factors will be discussed. Here we will focus on internal factors such as changes in attentional priority and strategic changes in anticipation of an event.

As we are looking for dynamic aspects of visual information storage in the brain, we will focus on research methods that can detect dynamic changes. This encompasses fMRI and EEG studies, as well as some single-cell monkey studies. Additionally, the focus will be on studies that use multivariate decoding methods. this is because multivariate decoding techniques allow analysis of WM storage over time. Together this will provide a general overview of what we know about dynamic aspects of VWM and where more or different research is necessary to draw conclusions about dynamic VWM storage.

### Univariate vs multivariate visual working memory research

Neural activity WM analysis techniques can be subdivided into two main types, univariate and multivariate.

Univariate analysis is focused on detecting increases in activity (Riggall & Postle, 2012). For example, in single-cell research, one measures the activity of a neuron and studies whether the activity is related to a specific task. A similar thing is done in EEG research, where a specific EEG response, an event related potential, is studied to decipher whether and when a specific event is processed in the brain. Within WM research, univariate analysis measure whether and where there is a sustained increase in neural activity during a retention period.

During working memory retention, multiple processes are occurring. For example, directing inward attention toward the stored item, processes underlying the mental load the working memory process takes, and finally, the visual information itself. Since univariate analysis methods only indicate an increase in activity in a certain brain area, it is sometimes unclear which of the concurrent processes is occurring.

Multivariate analysis techniques solve this problem. Here, the activity of multiple measures and how they relate to each other is measured. This makes multivariate pattern analysis (MVPA) possible. Here, the specific neural patterns related to WM storage can be uncovered. This solves two problems. First, multivariate patterns enable classification analyses, which provides information about the kind of process that is taking place. Second, multivariate analysis enables analysis of WM that might not be characterized by sustained increased firing, but specialized neural patterns. For example, sustained firing as measured by univariate analysis decreases in sensory regions, while stimulus-specific information can still be extracted through multivariate analysis (Linden et al., 2012; Riggall & Postle, 2012). Multivariate analyses are most often utilized in fMRI research, as well as some EEG studies.

In short, univariate studies provide information about which brain regions show sustained increase in information during a WM retention period. This can reflect different WM processes, such as attention, effort and information storage. However, they do not provide information about how visual information is stored (over time). Multivariate analysis can provide insight into how visual information is stored. Additionally, multivariate analysis can uncover neural representations that are characterized by neural patterns instead of sustained increased activity.

## **Intrinsic characteristics of visual working memory storage**

Before discussing which internal and external factors might influence neural representations in VWM, the intrinsic stability of visual working memory storage must be discussed. This entails potential changes that occur when simply storing an item in visual working memory. This includes VWM storage through persistent activity and dynamic coding, as well as neural drift and noise.

### *Persistent activity*

In univariate macaque single-cell activity research, persistent activity during the retention period of a delayed recall task can be seen in the prefrontal cortex (Compte et al., 2000; Constantinidis et al., 2018 Kamiński & Rutishauser, 2020). Here, neurons showed a stimulus-specific sustained increase in fire rate over the entire delay period. Similar results were found in invasive single-cell recordings in humans (Kamiński et al., 2017). Here, delays where participants stored multiple images in WM were characterized by persistent neuronal fire rate in prefrontal and medio temporal regions. Prefrontal activity was stable across different stimuli and was mostly related to memory load. Hippocampal and amygdala neurons on the other hand showed stimulus-specific persistent activity (Kamiński et al., 2017; Kornblith et al., 2017).

Similarly, univariate fMRI VWM research argues in favor of the activity-persistent WM processing. In a study, visual working memory retention was established through sustained neural activity (Curtis & D'Esposito, 2003; Curtis & Sprague, 2021). Here, active VWM retention was characterized by neurons in the prefrontal cortex showing increased sustained neural activity. In addition, EEG studies show persistent gamma oscillations in the prefrontal cortex, associated with working memory maintenance.

Since these were univariate analyses, it is unclear whether these persistent neuronal oscillations contained working memory information, or reflected supporting working memory processes, such as attention or effort. In fact, human studies that employ both univariate and multivariate analysis consistently show an absence of stimulus-specific activity in prefrontal regions even though there is increased activity (Linden et al., 2012; Riggall & Postle, 2012). So, while there is sustained increased activity in these regions during human WM retention, they likely reflect supporting processes such as attention and/or effort.

In short, prefrontal areas show increased sustained activity during a WM retention period. This is visible through sustained cell firing, increased fMRI BOLD, and gamma

oscillations. In macaques, this prefrontal sustained firing is stimulus-specific. In humans, increased activity in prefrontal areas likely reflect processes such as attention and effort.

### Dynamic coding

Later multivariate studies find that stimulus-specific information might be encoded in more dynamic patterns in sensory areas (Sreenivasan et al., 2014; Curtis & Sprague, 2021). So, while persistent activity can be seen in prefrontal areas during visual working memory maintenance, other regions might employ more dynamic methods of encoding.

For example, fMRI studies employing multivariate analyses, such as MVPA, show that visual information can be encoded through neural patterns, as opposed to increased persistent activity (Christophel et al., 2018; Riggall & Postle, 2012). This dynamic population coding is consistently seen in multivariate studies (Meyers, 2018). For example, in a multivariate EEG study, decoding models perform best when tested and trained on the same time interval during a delay (Chota et al., 2023).

Some studies also indicate that there are differences in neural patterns in fMRI research humans and single-cell recordings in primates between the encoding and maintenance phase (Iamshchinina et al. 2021; Spaak et al. 2017). Consequently, there is a shift in representation between these time periods. In single-cell macaque research, neurons appear to change or invert their coding of WM representations between the encoding and maintenance phase.

So, while neural representations stay stable on a larger neural population level, there is still some aspect of dynamic coding present, as representations appear to change over time.

### Neural drift & decay

Furthermore, neural representations can change over time through the intrinsic build-up of noise. While VWM is regarded as relatively stable, there is still a loss in precision over time, as shown in response error (Rademaker et al., 2018). This temporal loss of precision can be explained by increasing noise in the neural firing patterns of neurons (Bays, 2014).

In addition to general noise and decay, neural representations of stimulus-specific information can drift over time. Here, the neural representation changes over time to another irrelevant, but meaningful, representation. Evidence for this was found in monkey data, where the neural tuning of spatial representations predicted response error (Wimmer et al., 2014). In this study, spatial information was initially stored in neural representations that preferred that spatial location, and drifts in this representation (clockwise or counterclockwise) predicted



which way a response error would fall. This implies that neural representations can change over time. Furthermore, it shows that response is not only driven by the originally remembered stimulus, but also by how the remembered stimulus representation changes in VWM.

In a multivariate human fMRI study, orientation information stored in visual working memory was represented through neural activity patterns in the visual cortex (Lim et al., 2019). Participants were shown a target and probe orientation. They were then asked if the target matched the probe or not, resulting in a match/nonmatch response. Neural drifts away from the target orientation predicted incorrect nonmatch responses. Furthermore, neural drifts toward the probe orientation predicted incorrect match responses. In a multivariate EEG study, neural drift was observed over multiple time periods in a trial (Wolff et al., 2020). During the encoding and early maintenance phase, this neural drift was unrelated to eventual response error. Toward the end of the trial, neural drifts were biased toward response error, which occurred at the end of the trial. This indicates that neural drift might be a continuous process, where shifts occur over time. At a moment of response, this neural drift then affects behavior (response error).

Thus, neural drifts in visual working memory affect behavioral response. This has implications for visual working memory research. Since, if the currently held representation is a better predictor for behavior than the originally encoded stimulus, using this shifted item might be more helpful in behavioral research questions. Furthermore, if representations shift over time, this needs to be considered when decoding a stimulus from VWM. Since, if the neural representation has drifted away from the original stimulus, this will impact how well the item is decoded from the cortex. Understanding when and how neural drifts occur will therefore not only provide understanding into the inner workings of visual working memory, but also help refine VWM research.

In conclusion, stable persistent activity in the prefrontal cortex might underlie executive working memory processes. However, stimulus-specific information is coded in more complex neural patterns. These patterns appear to change over time. These changes can occur through spontaneous noise and decay in representations. Additionally, there is evidence for neural representations to spontaneously but systematically drift toward other meaningful representations. While both noise and neural drift affect behavior, neural drift can be more easily analyzed and might provide more insight into the dynamic changes VWM representations are subject to. Overall, even through simple VWM retention, dynamic changes are at play that affect how a stimulus is stored and consequently drive behavior.

## Effects of external factors on visual working memory representation

Aside from intrinsic changes in WM representations, external factors can also affect how visual information is stored in WM. In the stimulus-rich environment we live in, there is constant stream of visual information entering the brain. An item stored in VWM needs to be robust to this outside visual interference. Here, we will discuss how VWM representations might change in the face of external factors, such as visual interference.

### Interference in the early visual cortex and intraparietal sulcus

Apart from spontaneous changes in neural representation, dynamic representational shifts can also be caused by external factors. In fMRI studies, visual distractors affect neural representation of visual information in the early visual cortex (EVC). Visual items stored in VWM can be decoded from both EVC and the intraparietal sulcus (IPS) during the delay period (Bettencourt & Yu, 2016; Christophel et al., 2018; Rademaker et al., 2019). However, if a distractor is introduced during this delay period, the stimulus representational strength lowers.

Within this paradigm, different studies show varying results. For example, in one study, the stimulus could not be decoded when a visual distractor was introduced during the delay period (Bettencourt & Xu, 2016). Another study showed a decrease in decoding strength of remembered orientations in EVC only if distractors were heavily salient, such as a face (Rademaker et al., 2019). However, a later re-analysis showed decreased decoding strength in the EVC with Fourier noise distractors as well (Iamshchinina et al., 2021). In the first analysis by Rademaker et al. (2019), the decoding model was trained on neural patterns during the delay period, and in the analysis by Iamshchinina et al. (2021) the model was trained on data from a separate mapping period where a participant looked at different orientations. This shows that that sensory-like representations in the EVC might be more vulnerable to interference, while mnemonic representations formed during a maintenance phase might be more robust.

Other studies found that the neural representation in EVC doesn't diminish when a distractor is introduced, but is rather biased toward the distractor (Hallenbeck et al., 2021; Lorenc et al., 2018). Here, distractor orientations had a small attractive bias on the orientation stored in VWM. Similar to other research, this attractive bias effect was only measured in the EVC, and not the IPS.

Neural firing patterns in the IPS appear relatively unaffected by visual interference during a retention period (Lorenc et al., 2018; Rademaker et al., 2019). Using multivariate analysis, visual information can be decoded from the IPS before, during, and after visual interference. Thus, this region might support a more stable manner of working memory storage, robust in the face of distraction and interference (Lorenc et al., 2021). This parallel storage system might be a more robust manner of storing information in VWM. Through this mechanism, behavioral performance could remain stable while filtering outside influences. There is even some evidence to suggest that the IPS stores visual information in a more low-resolution format than the EVC (Chunharas et al., 2023).

Thus, the EVC stores a high-resolution image of a visual working memory item, but is susceptible to disturbance. To counter this, a low-resolution version of the same information could be stored in a more stable region less affected by disruptions. Together, this parallel storage method ensures information is not lost in the external-factor rich environment around us.

In short, outside distractors and interference can temporarily weaken or change VWM representation of remembered stimuli. This results in a diminished representational strength of the remembered stimulus in the EVC. This diminishing effect is modulated through the stimulus-type of the used interference. Diminished representational strength during interference is less prominent in other regions, such as the IPS. Competition within the EVC between working memory and visual input processing might mediate neural representation suppression. This leaves some questions about how this suppression comes into effect and whether the neural patterns disappear completely or simply weaken.

#### *Visual probes uncover possible low-activity representations.*

Interestingly, external visual factors can also positively impact how well visual information can be decoded from VWM (Wolff et al., 2015). In a multivariate EEG study, neural oscillations representing visual information storage decrease over time. However, when presenting a clear white visual probe, the original stimulus could be decoded from the EEG signal again. After this, the decoding strength dropped below baseline again. The same technique was used to decode visual information in the EEG study regarding neural drift (Lim et al., 2019). While a clear white distractor is unlikely to occur during a maintenance phase outside of research experiments, it does give some insight into how neural information might be represented in VWM over time. Since, even though neural representations for an item weaken to below measurement baseline, the information might still be encoded in the brain.

Here, a simple visual probe (without any orientation information) caused a short increase in the neural patterns in which the information was originally stored. The brain might employ dynamic storage methods to optimize energy distribution and store information in less activity-driven methods while retaining the information in other ways.

One explanation for this phenomenon comes from the activity-silent account (Wolff et al., 2015; Kamiński & Rutishauser, 2020; Stokes 2015). Here, it is hypothesized that neural representations are stored in activity-silent codes over time. Here visual information is not represented through neural firing patterns, but temporary changes in synaptic weights. In this case, a strong visual probe is run through these synaptic connections, highlighting the neural pattern encoded in these synaptic weights. One important note is that this theory is based on neural information not being decoded in certain conditions or after a certain time. It is also possible that the information is still encoded in neural patterns too weak or different from the original representation to be picked up by analysis methods (Rademaker & Serences, 2017). Here, the ping could simply increase all activity in the EVC, including pushing the stimulus-specific patterns above baseline.

Thus, while a ping in activity after a visual probe could imply the presence of activity-silent mechanisms, they could also reflect an increase of neural activity patterns too weak to detect normally.

External influences, such as visual interference, can affect the representational strength of items stored in VWM. Studies using fMRI show that visual interference can alter neural representation in the EVC. The EVC may show diminished representational strength during interference, while the IPS seems less affected, potentially suggesting a parallel storage system. Competing processes between working memory and visual input processing in the EVC may mediate neural representation suppression. However, external visual factors, like a clear white visual probe, can positively impact decoding visual information from VWM. This could either reflect activity-silent codes, or general strengthening of diminished neural patterns.

### **Effects of internal factors on visual working memory representation**

Aside from general storage mechanisms and external effects, internal effect can also affect how dynamic storage occurs. We often move through stimulus-rich environments, but our own internal processes also play a role. For example, directing attention or changing an internal strategy in anticipation of an event.

*Attentional demands affect distribution of neural resources.*

Visual working memory can store and maintain multiple items at the same time (Vogel et al., 2001). However, not all items are always equally relevant at any given time. For example, when you walk through a store, and need to find milk first, and then cookies. Both ‘milk’ and ‘cookies’ could be stored in VWM, but one is currently relevant, and the other is not. It might be useful for the brain to distribute resources based on this task-relevant demand. Here, a currently relevant memory item might receive additional attention and/or resources to optimize behavior. The currently irrelevant item would then receive less resources while attending the relevant item. When this item becomes relevant after a while (after you have found the milk and move on to cookies) this item could then receive the additional resources. Thus, dynamic changes in neural representation in response to attentional demands might be a useful method of storing multiple items in visual working memory.

These dynamic changes in neural representation in response to changes in attention can be studied through a double retro-cue design (Christophel et al., 2018; Yu et al., 2020). Here, a participant remembers two or more stimuli (e.g. two orientations), after which a retro-cue indicates which of the two stimuli is going to be relevant for an upcoming task. This causes this cued item to become actively attended (Attended Memory Item – AMI). After this first delay and response period, a second retro-cue is shown. This can either be the previously cued item, or the other previously un-cued item. This ensures that the un-cued item in the first delay is not discarded. Since the un-cued item is not relevant in the first delay, but cannot be discarded, it becomes the not actively attended item (Unattended Memory Item – UMI). Through analyzing differences in neural representation between these two items, dynamic effects of attention can be analyzed.

Studies using this paradigm show differing results. Some studies are able to decode the AMI from the EVC using multivariate fMRI techniques, but not the UMI (Christophel et al., 2018). In this study, the IPS contained information about both the AMI and the UMI. This suggests that information is divided and distributed across brain regions in accordance with internal attentional demands. A later study did find evidence for the UMI in the EVC in the same dataset (Iamshchinina et al., 2021). This was attained by training the decoding model on the stronger attended (AMI) representations, and training them on the UMI. This further shows that an absence of multivariate evidence in studies does not indicate an absence of information in neural regions. This is further exemplified by findings by Yu et al. (2020) and

van Loon et al. (2018) where the representational format of the UMI appeared to change when becoming the UMI. This would also result in the UMI not being decoded by a decoding model trained on the initial representation. This phenomenon will be further discussed in a later section.

One study used both multivariate fMRI and EEG methods to analyze the AMI and UMI in visual working memory (Rose et al., 2016). Similar to previous experiments, evidence for the UMI dropped below baseline in category-specific areas after presentation of the first retro-cue. If the UMI was cued in the second delay, this effect reversed. So, evidence for both memory items in VWM differed depending on which is relevant at a specific moment. In the EEG experiment, they applied a pulse of a transcranial magnetic stimulation (TMS) to the brain region related to storing the information after the first and second retro-cue. This pulse temporarily increased the classifier performance for the UMI to above baseline. Thus, the information for the UMI was still stored in this brain region in some capacity, even though the classifier could not detect it without the probe. This phenomenon is not dissimilar to that seen in the study by Wolff et al. (2015). In this study, a strong visual probe temporarily increased the pattern distinctiveness of an item stored in visual working memory. Whether this is a result of under-baseline activity being strengthened to above-baseline through the probe or another process is unclear and material for discussion.

In short, the brain appears to be able to distribute neural resources, such as representational strength to memory items based on task-relevance. This representational strength effect is most prominent in the EVC, a brain area already implicated in adapting representational strength depending on different (outside) factors.

#### *Attentional demands affect neural representational formats.*

Attention demands appear to affect how many neural resources are distributed to different memory items. Interestingly, there is also some evidence to suggest that attended and unattended memory items might be stored in different representational formats, depending on their current relevance.

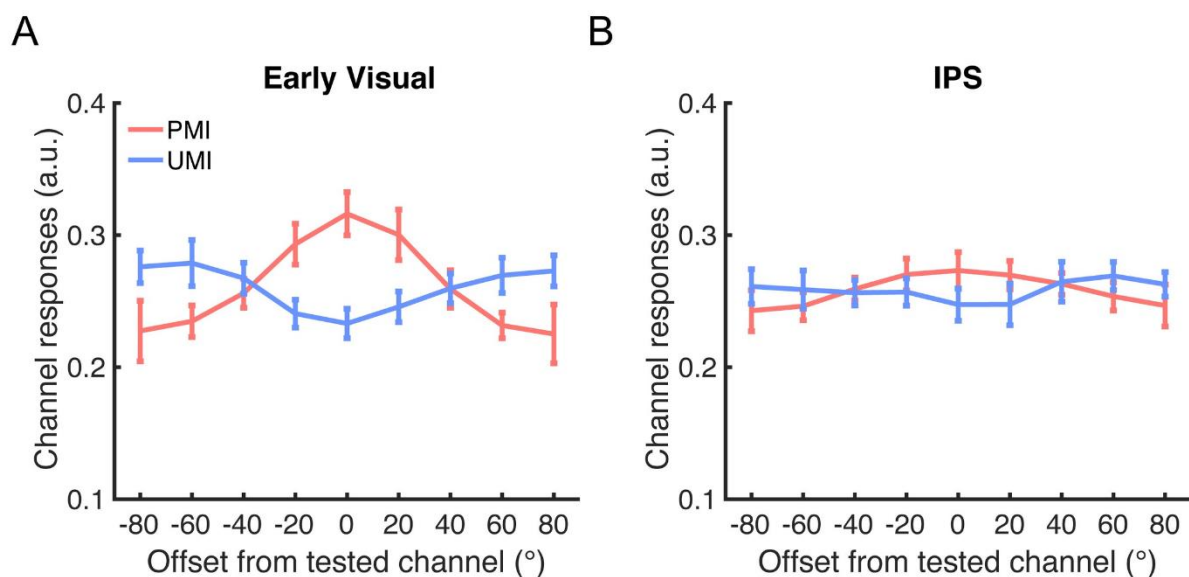
In a search experiment by van Loon et al. (2018) participants were shown two objects. A cue then informed them which of the two items they needed to search for first, and which second. This meant that the first object they had to search for was currently relevant, while the item that they had to search for second was only prospectively relevant. Similar to a double retro-cue design, this meant one item would be currently attended (AMI), while the other would not be currently attended (UMI). The main difference to a retro-cue design is that in

this study the UMI had a 100% chance of being relevant later, while this chance is lower in a retro-cue design (usually 50%). Multivariate fMRI decoding uncovered the UMI stored in an opposite format to the AMI in the posterior fusiform cortex, a brain area related to representing object categories. A study by Yu et al. (2020) showed similar results. In a double retro-cue design, both the AMI and UMI were decoded from the EVC. However, after the presentation of the first retro-cue the representational strength of the UMI dropped. Furthermore, they found that the UMI was stored in an opposite representational format as the AMI in the EVC (i.e. a 90-degree UMI would be represented the same as a 0-degree AMI). A similar effect was observed in the IPS (Figure 1.). So, attentional divide not only dynamically changes *where* information is stored, but also *how* this information is stored.

An EEG study provided further evidence for this theory (Wan et al., 2020). As in the previous fMRI studies, the representational format of the UMI changed into one opposite to the AMI after a retro-cue made one currently relevant). If the second retro-cue made the UMI relevant, this change was reversed.

**Figure 1.**

*Inverted encoding model (IEM) channel responses of the AMI and UMI in the early visual cortex and intraparietal sulcus. (Yu et al. 2020).*



*Note. IEM channel responses of the AMI (labelled as PMI) and UMI decoded from the ECV (A) and IPS (B). Decoding model was trained on the AMI. A channel response peak indicates evidence for the data to align with a certain orientation. In both regions, the channel responses related to the AMI peak at the originally shown orientation. The channel responses of the UMI dip at the originally shown orientation, and peak at the opposite orientation (90 degrees further). This means the UMI is represented in an opposite format as the AMI.*

Thus, unattended memory items might change from their initial representational format to one opposite to attended memory items. This ‘priority-based remapping’ might be a dynamic process that shifts representations formats back and forth in accordance with attentional demands. This remapping of representational formats might enable the brain to store currently unattended items in concurrently with attended memory items, while distributing most resources to the attended item.

#### *Adapting WM representations in anticipation of response*

Interestingly, this opposite encoding effect manifested itself a few seconds before recall, not immediately after the cue (Figure 2.) (Yu et al., 2020). A similar effect was found in the study of van Loon (2018), where representations of the AMI increased right before response. This implies that opposite encoding is a mechanism the brain employs in anticipation of a response. Here, strengthening the brain strengthens the representation of the AMI to optimize behavior. Storing the UMI in an active, yet opposite representational format might be a way to retain high-resolution representations for both, while not having the two interfere with each other. Additionally, strengthening representations in anticipation of response shows the brain can decrease and reactivate mnemonic representations based on behavioral demand.

There is also some evidence to suggest that the brain allocates different neural resources in anticipation of an action (Henderson et al., 2022). In one study, participants were tasked with remembering the spatial location of a dot. After a delay, they were shown a circle with two halves of different colors. Then another delay, and another circle. At this second circle participants had to reply in which half of the circle the original dot was located. The circle could be rotated in any orientation. In one half of the trials, the first circle was the same orientation as the second one. Participants were also informed via a cue whether this was the case. This meant that in half of the trials, participants could anticipate their response at the second (response) circle. In these trials, researchers found less spatial information about the remembered dot in early visual and parietal regions. Additionally, a representation of the planned response appeared in primary motor, somatosensory, and premotor cortex. This implies that the brain can change storage locations and formats depending on anticipated behavior.

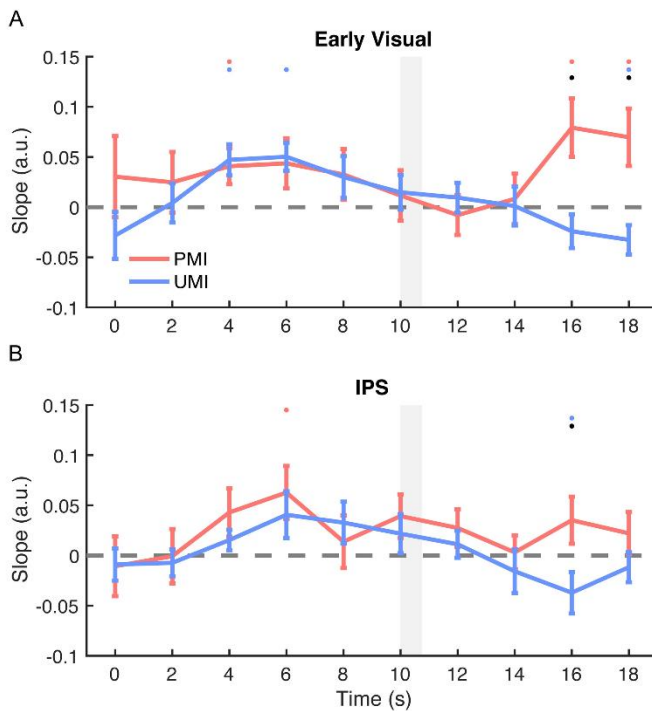
Thus, WM representations can strengthen and/or change in anticipation of response. This can be attained through strengthening neural representations of the relevant memory items. Additionally, the brain can shift and change storage locations and formats to best fit



behavioral needs. This way, the brain optimizes resource distribution depending on behavioral demands.

**Figure 2.**

*IEM slope as a measure of representational strength for the AMI and UMI in EVC and IPS. (Yu et al., 2020).*



*Note. IEM reconstruction slopes for the AMI (labelled PMI) and UMI over time. A. early visual cortex. B. Intraparietal sulcus. Timeseries starting right after stimulus presentation (0s), through cue presentation (10s) and until recall (18s). IEM models trained on the AMI. In both the EVC and IPS, IEM slopes increase for the AMI and UMI. For the UMI, the IEM channel responses were encoded in an opposite format as the EVC, as shown in the negative slope. This implies that the brain strengthens representational formats in anticipation of response, strengthening both the AMI and UMI.*

*Strategic changes as opposed to reactive changes in anticipation of future interference.*

As mentioned previously, neural representational strength decreases below baseline when distraction is introduced (Bettencourt & Xu, 2016). However, this effect was only present when participants were sure a distractor was going to appear (100% distractor trials). If the probability of a distractor was lower (50/50), the original stimulus could still be decoded during the distraction period. This implies that the drop in representational strength is not a reactive process, but an internal strategic one. Here, a participant strategically alters which neural recourses are used in anticipation of a future event. This also complicates research on external effects as one cannot rule out internal strategic changes affecting neural representations and locations. It also raises questions about how an experiment should be set

up. Since, in a blocked experiment design, anticipating an upcoming event might cause more internal strategic processes to come into account, as opposed to only external ones. While this provides insight into how internal factors might affect how the brain responds to external factors, it does not provide a clear separation between the two.

In conclusion, internal factors can affect how and where visual information is stored during VWM retention. This can be due to attentional demands. Here occipital resources are more widely allocated to attended visual information instead of unattended visual information. It can also be due to strategic allocation in anticipation of future behavior or interference. Internal factors might also play a role during interference of external factors and therefore cannot be studied completely separately.

### **Brief overview and speculation**

Visual working memory storage is subject to dynamic processes that either occur naturally, or as a result of internal and/or external factors.

When simply storing an item in visual working memory, stimulus specific information is likely stored in sensory areas. This is either through persistent activity, but more so through patterns of neural activity, without necessarily resulting in increased neural activity. These neural population codes can change over time. In macaque research, individual neurons can change or invert their firing patterns to support VWM retention (Iamshchinina et al. 2021; Spaak et al. 2017).

Representations over time can also change through noise effects. Here, noise builds up in the neural patterns that represent the visual information, resulting in increased response error. Another naturally occurring process is that of neural drift, here neural representations shift to that of similar visual information, biasing both neural representations and behavior.

Thus, both stable and dynamic mechanisms are at play during visual working memory retention.

During distraction and interference, neural representation strength decreases in the EVC. After interference, there is also evidence of visual information being biased toward the distractor image if the two are similar (Lorenz et al., 2018). On the other hand, representations in the IPS remain relatively stable. The brain utilizes both stable and dynamic storage systems in parallel to optimize visual information retention while dividing resources between multiple stimuli.

Strong visual input can also further activate neural representations. When faced with a

strong visual probe, previously diminished neural oscillations become visible again. The mechanism as to how this happens is unclear.

Internal factors can affect how information is stored in working memory. For example, the brain distributes different neural resources to different items depending on their behavioral relevance at a given time. This is characterized by items that are currently relevant being represented more strongly in the EVC. Here, prospectively relevant items are stored in weaker representational patterns in the EVC. Furthermore, the representational format of prospectively relevant items can shift to one opposite to that of currently relevant items. This representational change is reversed when the prospectively relevant item becomes currently relevant. Both the representational strength and the representational shift changes could be modulated through attention.

Neural pattern strength could also be modulated when anticipating an action or interference. For example, when anticipating interference, the representational strength of a memory item drops in the EVC in anticipation of stimuli competing for resources in this area.

#### *The role of the early visual cortex in visual working memory*

A brain area where internal and external factors regularly affect neural representation is the EVC (Bettencourt & Yu, 2016; Rademaker et al., 2019). When faced with visual interference neural representations of remembered visual items weaken. Furthermore, the representational strength and format appears to change based on current behavioral demands. In addition, there are differing reports on whether neural representation strength in the EVC predicts behavior (Xu, 2020). So, what does this tell us about the function of the EVC?

One explanation is that the EVC might not be essential for working memory storage (Xu, 2020). Since, if the EVC is essential, one would not expect representational strength to drop in the face of (anticipated) interference (Bettencourt & Xu, 2016). Furthermore, response error remained regardless of neural representational strength. A similar effect was observed in the study by Rademaker et al. (2019). Here, behavioral response did not drop in an experiment where EVC representation strength dropped, but did so in a secondary experiment where a drop in representational strength in the IPS was observed. These results might imply that the information held in the EVC are not essential for VWM storage, as representations are vulnerable to modulating factors and appear to not always guide behavior. Instead, the EVC might pose as a hub of sorts, where concurrent visual information from the environment and VWM come together and can be compared. This then makes the EVC vulnerable to competing stimuli from both sources.

### *Changing representational codes during interference?*

However, a drop in decoding accuracy during interference in the EVC does not necessarily mean that information is lost. One important finding that might affect how we look at a drop in representational strength in the EVC during interference is that of changing representational formats (van Loon et al., 2018; Wan et al., 2020; Yu et al., 2020). Some studies suggest that the EVC can change the original representational format of visual memory items to optimize storage when task demands change. It is possible that a similar effect is occurring during interference. Here, neural representations of visual information might change formats to not be diminished by the incoming visual signal. Representing mnemonic representations and concurring visual information in different representational formats might be a way the brain can retain both kinds of information.

From a decoding stance, a change in representational format during interference would mean a decoding model trained on the original format would be unsuccessful in decoding the stimulus during the interference phase. Training a decoding model on the data during interference and testing it on the same data in a leave-one-out method would provide insight into whether representations still exist and might have changed formats.

Since the incoming visual signal would introduce non-relevant neural activity in the EVC, this would need to be done using many trials to increase power. An interleaved and blocked design would provide different insights into the possible workings of this mechanism. In a blocked design, a participant would be able to strategically alter which neural mechanisms are utilized in anticipation of interference. Analyzing how representational formats might change here would provide further insights into how and when the brain alters representational formats in response to top-down processes. In an interleaved design, a participant would be worse at anticipating whether interference will occur. Therefore, utilizing this design would provide insights in how and whether representational formats change in response to ‘unexpected’ bottom-up interference.

Thus, different research methods within interference studies would provide a better understanding to whether a drop in representational strength during interference reflects an absence or a change in neural representations.

### *Activity-silent codes as a storage mechanism in absence of neural pattern activity*

Another explanation for the drop in representational strength in the EVC in absence of a drop in behavioral performance comes from different storage types. While current VWM

studies focus on multivariate pattern analysis of neural representations, there is a hypothesis that visual information might be stored in activity-silent patterns. Here, a visual item is not represented through neural activity patterns, but temporary changes in synaptic weights (Wolff et al., 2015; Kamiński & Rutishauser, 2020; Stokes 2015). Within this theory, visual information can be accessed and used without the need for constant pattern activity during VWM maintenance. Support for this theory comes from studies that make use of a ‘pinging’ technique (Rose et al., 2016; Wolff et al., 2015). These studies mentioned earlier observed an increase in decoding strength after a strong probe activated the previously below-baseline neural patterns. This could then be the result of information flowing through the temporary synaptic weights, highlighting the embedded neural pattern.

This activity-silent theory is further supported by research that shows a relationship between visual working memory and long-term memory mechanisms (Oberauer, 2022; Rose & Chao, 2022). Here, an item not currently attended might be temporarily stored in long-term memory, instead of working memory. This is different than the traditional activity-silent account, where items are still stored in WM. However, another study provided a dissociation between the two (Chao et al., 2022). Thus, a long-term memory account of unattended WM storage is still debated.

A complicating factor within the activity-silent hypothesis is that it is based on an absence of neural pattern recognition through MVPA methods during VWM retention. The assumption is then that there are no patterns. Consequently, the increase in decoding strength a pinging technique causes must be through another mechanism. However, it is possible that the neural patterns and representations are still there, but lower in strength. Furthermore, since neural representations appear to shift over time, it is also possible that the stimulus that is being decoded is now (slightly) different from the original stimulus that is used in the decoding model. This would also decrease the decoding strength of the original stimulus. Overall, this would mean the representations are still there but cannot be detected through MVPA analysis. A pinging technique would then increase all neural activity, and increase neural patterns above baseline detection.

In fact, a re-analysis of the pinging study by Wolff et al. (2020) hinted at a lack of representation strength being the result of low statistical power, not absence of activity (Barbosa et al., 2021). They showed that when different analyzing methods are used, the original memory items can be decoded, or decoding comes close to statistical significance. It must be said that this also does not exclude the possibility of activity-silent states, as both activity-based and activity-silent aspects of VWM could occur simultaneously.

It would be interesting to understand whether and how activity-silent mechanisms are utilized in VWM retention. Current pinging (either through visual probe or TMS) use a single probe during a maintenance period. It might be interesting to use multiple probes during a maintenance phase (at different intervals) and see whether the pinged representation changes over time. Since, we know that active neural representations shift over time. Perhaps if the representation highlighted through the pinging technique shows stable representations, it would provide evidence for an activity-silent code, consolidated during the encoding phase. Though, the possibility of active and activity-silent codes existing synchronously would complicate this, as active (dynamic) representations would also be pushed. Additionally, if activity-silent codes also endure dynamic changes over time, this effect would also not be observed. Still, utilizing multiple probes and analyzing VWM during a maintenance phase over multiple time intervals would provide valuable insight into how VWM active and possible activity-silent codes change over time. It would also be interesting to see how the ping would affect recall. Since the ping temporarily increases representational strength, it would be interesting to see whether this would reduce response error. This would be done by comparing responses right after a ping with responses with no ping, or a much earlier ping. All in all, different research paradigms could provide valuable insight into which mechanism is actually activated through a ping, and whether they can affect behavior.

Thus, some studies suggest the EVC might not play an essential role in visual working memory storage. Instead, the EVC acts as a place where internal mnemonic representations and external visual information can come together and interact to support things such as template search. This theory is supported by studies where a drop in representational strength in the EVC do not necessarily cause a drop in behavioral performance, while this is the case for other regions, such as the IPS (Bettencourt & Xu, 2016; Rademaker et al., 2019). However, other studies do show a relationship between representational strength in the EVC and behavioral performance (Ester et al., 2013). Furthermore, information might be stored in the EVC through activity-silent codes or in different representational formats. That way, a high-resolution representation could be retained without taking up too many resources. Taken together, the EVC is a highly flexible brain area capable of storing and shifting many types of visual information. Understanding how these flexible processes occur in the EVC will help understand how multiple brain areas work together in sustaining WM representations.

### Recommendations for future research

Visual working memory is constantly adapting to external and internal factors. Therefore, studying the subject in static, whole-block, intervals will provide results that might not fully reflect the wide array of processes and mechanisms that underlie visual working memory. Furthermore, the way an experiment is set up might leave a participant with expectations about upcoming events, which can affect results.

First, it is important to remember the different internal processes that might occur during a visual working memory experiment. For example, anticipating an event might cause strategic changes to occur that affect where and how visual information is stored. This anticipatory effect will be strongest in a blocked experiment design, where trials of the same condition occur one after another. In an intermixed design on the other hand, a participant can anticipate an event with less accuracy, and condition-specific strategic representational changes might be diminished. Thus, if only external factors should be measured, an intermixed design might decrease the risk of internal factors having an effect. A blocked design still provides valuable insights into how internal processes might affect how VWM responds to external demands. Furthermore, by choosing to conduct both an intermixed *and* a blocked experiment, the added effect of internal anticipatory processes can be isolated. Hence, both blocked and intermixed designs can help provide insights on different aspects of visual working memory research. One should be aware of how the design they choose might affect visual working memory processes.

Second, VWM storage is highly flexible in representational strength, shifts, and format changes over time. Thus, by analyzing WM storage in one large maintenance or interference block might cloud decoding, as representations change over time. Furthermore, if representational formats change in response to internal or external factors, one might not be able to decode a memory item at all, if only using models trained on an initial encoding or maintenance phase. Therefore, analyzing VWM storage over time, instead of as a block, might increase how well information can be decoded from different brain areas. It will also provide valuable insights into when and how these different dynamic processes are utilized.

Third, one must be careful in choosing how to setup a decoding model. Since, as representations change over time, training on only the encoding or maintenance phase might cause subtle or large changes to be missed. For instance, if one observes a drop in representational strength in a specific condition or after a certain time. In this case, it might be interesting to train and test a decoding model on this specific time period. This way, if representational formats changed from the original encoding/maintenance phase, the

information could potentially still be decoded from this period.

Finally, another aspect of real-life VWM storage that is underrepresented in current research is the type of stimulus used in VWM research. Most studies employ a paradigm where one or more simple stimuli are remembered, or one or two aspects of a stimulus (color, orientation). However, in the outside world, these simple stimuli or aspects rarely occur by themselves. Instead, we move around in a stimulus and aspect-rich environment, with many colors, orientations, shapes, and object locations. In a dynamic VWM view, these many different aspects and stimuli might interact and alter representations differently than when only maintaining simple stimuli. Similarly, by utilizing different task types, new dynamic mechanisms of VWM storage might be uncovered.

### Conclusion

VWM appears to shift and change representational formats as well as modulate representational strength in response to internal and external factors. Many of these changes have not been studied yet, either through experiment design (i.e. stimulus/task choices) or analysis method (i.e. analyzing WM over an entire retention block). Understanding when and how these dynamic changes occur will provide valuable insights into how VWM is utilized and stabilized in a stimulus-rich environment. For this purpose, previous fMRI studies could benefit from temporal generalization techniques, as used in EEG research. Here, WM representations could be studied over time, and changes in representation over time could be uncovered. Future studies could employ both blocked and intermixed designs, to allow uncovering distinctions between strategic and responsive WM changes. Additionally, using stimuli and paradigms that more closely reflect the stimulus- and interference-rich environment we live in would provide a more realistic WM account. Taken together, this will not only help answer the *what* and *where* questions commonly answered in WM, but also the *when* question. Only by answering all three in a dynamic WM account, can we better understand how WM is constantly adapting to support our daily lives.



## References

- Barbosa, J., Lozano-Soldevilla, D., & Compte, A. (2021). Pinging the brain with visual impulses reveals electrically active, not activity-silent, working memories. *PLoS biology*, *19*(10), e3001436.
- Bays, P. M. (2014). Noise in neural populations accounts for errors in working memory. *Journal of Neuroscience*, *34*(10), 3632-3645.
- Bettencourt, K. C., & Xu, Y. (2016). Decoding the content of visual short-term memory under distraction in occipital and parietal areas. *Nature neuroscience*, *19*(1), 150-157.
- Mao Chao, C., Xu, C., Loaiza, V., & Rose, N. S. (2023). Are latent working memory items retrieved from long-term memory?. *Quarterly Journal of Experimental Psychology*, 17470218231217723.
- Chunharas, C., Hettwer, M. D., Wolff, M. J., & Rademaker, R. L. (2023). A gradual transition from veridical to categorical representations along the visual hierarchy during working memory, but not perception. *bioRxiv*, 2023-05.
- Chen, X., & Zelinsky, G. J. (2006). Real-world visual search is dominated by top-down guidance. *Vision research*, *46*(24), 4118-4133.
- Christophel, T. B., Iamshchinina, P., Yan, C., Allefeld, C., & Haynes, J. D. (2018). Cortical specialization for attended versus unattended working memory. *Nature neuroscience*, *21*(4), 494-496.
- Chota, S., Gayet, S., Kenemans, J. L., Olivers, C. N., & Van der Stigchel, S. (2023). A matter of availability: sharper tuning for memorized than for perceived stimulus features. *Cerebral Cortex*, *33*(12), 7608-7618.
- Compte, A., Brunel, N., Goldman-Rakic, P. S., & Wang, X. J. (2000). Synaptic mechanisms and network dynamics underlying spatial working memory in a cortical network model. *Cerebral cortex*, *10*(9), 910-923.
- Constantinidis, C., Funahashi, S., Lee, D., Murray, J. D., Qi, X. L., Wang, M., & Arnsten, A. F. (2018). Persistent spiking activity underlies working memory. *Journal of neuroscience*, *38*(32), 7020-7028.
- Curtis, C. E., & D'Esposito, M. (2003). Persistent activity in the prefrontal cortex during working memory. *Trends in cognitive sciences*, *7*(9), 415-423.
- Curtis, C. E., & Sprague, T. C. (2021). Persistent activity during working memory from front to back. *Frontiers in Neural Circuits*, *15*, 696060
- Ester, E. F., Anderson, D. E., Serences, J. T., & Awh, E. (2013). A neural measure of precision

- in visual working memory. *Journal of cognitive neuroscience*, 25(5), 754-761.
- Hallenbeck, G. E., Sprague, T. C., Rahmati, M., Sreenivasan, K. K., & Curtis, C. E. (2021). Working memory representations in visual cortex mediate distraction effects. *Nature Communications*, 12(1), 4714.
- Henderson, M. M., Rademaker, R. L., & Serences, J. T. (2022). Flexible utilization of spatial- and motor-based codes for the storage of visuo-spatial information. *Elife*, 11, e75688.
- Iamshchinina, P., Christophel, T. B., Gayet, S., & Rademaker, R. L. (2021). Essential considerations for exploring visual working memory storage in the human brain. *Visual Cognition*, 29(7), 425-436.
- Kamiński, J., & Rutishauser, U. (2020). Between persistently active and activity-silent frameworks: novel vistas on the cellular basis of working memory. *Annals of the New York Academy of Sciences*, 1464(1), 64-75.
- Kamiński, J., Sullivan, S., Chung, J. M., Ross, I. B., Mamelak, A. N., & Rutishauser, U. (2017). Persistently active neurons in human medial frontal and medial temporal lobe support working memory. *Nature neuroscience*, 20(4), 590-601.
- Kornblith, S., Quiroga, R. Q., Koch, C., Fried, I., & Mormann, F. (2017). Persistent single-neuron activity during working memory in the human medial temporal lobe. *Current Biology*, 27(7), 1026-1032.
- Lim, P. C., Ward, E. J., Vickery, T. J., & Johnson, M. R. (2019). Not-so-working memory: Drift in functional magnetic resonance imaging pattern representations during maintenance predicts errors in a visual working memory task. *Journal of Cognitive Neuroscience*, 31(10), 1520-1534.
- Linden, D. E., Oosterhof, N. N., Klein, C., & Downing, P. E. (2012). Mapping brain activation and information during category-specific visual working memory. *Journal of neurophysiology*, 107(2), 628-639.
- Lorenc, E. S., Sreenivasan, K. K., Nee, D. E., Vandenbroucke, A. R., & D'Esposito, M. (2018). Flexible coding of visual working memory representations during distraction. *Journal of Neuroscience*, 38(23), 5267-5276.
- Meyers, E. M. (2018). Dynamic population coding and its relationship to working memory. *Journal of neurophysiology*, 120(5), 2260-2268.
- Oberauer, K., & Awh, E. (2022). Is there an activity-silent working memory?. *Journal of cognitive neuroscience*, 34(12), 2360-2374.
- Rademaker, R. L., Chunharas, C., & Serences, J. T. (2019). Coexisting representations of

- sensory and mnemonic information in human visual cortex. *Nature neuroscience*, 22(8), 1336-1344.
- Rademaker, R. L., Park, Y. E., Sack, A. T., & Tong, F. (2018). Evidence of gradual loss of precision for simple features and complex objects in visual working memory. *Journal of Experimental Psychology: Human Perception and Performance*, 44(6), 925.
- Rademaker, R. L., & Serences, J. T. (2017). Pinging the brain to reveal hidden memories. *Nature neuroscience*, 20(6), 767-769.
- Riggall, A. C., & Postle, B. R. (2012). The relationship between working memory storage and elevated activity as measured with functional magnetic resonance imaging. *Journal of Neuroscience*, 32(38), 12990-12998.
- Rose, N. S., & Chao, C. M. (2022). Hippocampal involvement in working memory following refreshing. *Cognitive neuroscience*, 13(3-4), 215-217.
- Rose, N. S., LaRocque, J. J., Riggall, A. C., Gosseries, O., Starrett, M. J., Meyering, E. E., & Postle, B. R. (2016). Reactivation of latent working memories with transcranial magnetic stimulation. *Science*, 354(6316), 1136-1139.
- Roux, F., & Uhlhaas, P. J. (2014). Working memory and neural oscillations: alpha-gamma versus theta-gamma codes for distinct WM information?. *Trends in cognitive sciences*, 18(1), 16-25.
- Spaak, E., Watanabe, K., Funahashi, S., & Stokes, M. G. (2017). Stable and dynamic coding for working memory in primate prefrontal cortex. *Journal of neuroscience*, 37(27), 6503-6516.
- Sreenivasan, K. K., Curtis, C. E., & D'Esposito, M. (2014). Revisiting the role of persistent neural activity during working memory. *Trends in cognitive sciences*, 18(2), 82-89.
- Stokes, M. G. (2015). 'Activity-silent' working memory in prefrontal cortex: a dynamic coding framework. *Trends in cognitive sciences*, 19(7), 394-405.
- van Loon, A. M., Olmos-Solis, K., Fahrenfort, J. J., & Olivers, C. N. (2018). Current and future goals are represented in opposite patterns in object-selective cortex. *elife*, 7, e38677.
- Vogel, E. K., Woodman, G. F., & Luck, S. J. (2001). Storage of features, conjunctions, and objects in visual working memory. *Journal of experimental psychology: human perception and performance*, 27(1), 92.
- Wan, Q., Cai, Y., Samaha, J., & Postle, B. R. (2020). Tracking stimulus representation across a 2-back visual working memory task. *Royal Society open science*, 7(8), 190228.
- Wimmer, K., Nykamp, D. Q., Constantinidis, C., & Compte, A. (2014). Bump attractor

- dynamics in prefrontal cortex explains behavioral precision in spatial working memory. *Nature neuroscience*, *17*(3), 431-439.
- Wolff, M. J., Jochim, J., Akyürek, E. G., Buschman, T. J., & Stokes, M. G. (2020). Drifting codes within a stable coding scheme for working memory. *PLoS biology*, *18*(3), e3000625.
- Wolff, M. J., Ding, J., Myers, N. E., & Stokes, M. G. (2015). Revealing hidden states in visual working memory using electroencephalography. *Frontiers in systems neuroscience*, *9*, 123.
- Xu, Y. (2020). Revisit once more the sensory storage account of visual working memory. *Visual Cognition*, *28*(5-8), 433-446.
- Yu, Q., Teng, C., & Postle, B. R. (2020). Different states of priority recruit different neural representations in visual working memory. *PLoS biology*, *18*(6), e3000769.