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Dissociating Oscillatory and Aperiodic EEG Dynamics in Visual Working Memory

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Abstract

Visual working memory (VWM) allows visual information to be temporarily maintained, but its capacity is limited. Alpha-band EEG activity is often interpreted as a neural marker of VWM. However, traditional band-limited analyses may mix oscillatory alpha activity with the broadband aperiodic component of the EEG signal. Because of that, this thesis examines whether oscillatory and aperiodic EEG activity show different patterns during encoding and maintenance in VWM. Behavioral and EEG data were analyzed from a sequential delayed-estimation color-wheel task. Here, participants remembered one, three or five colored items. Later, participants reported the color of a probed item. Behavioral performance was assessed using absolute recall error. EEG analyses tested aperiodic phase differences, posterior alpha modulations and whether traditional alpha effects remained in decomposed oscillatory alpha peak amplitude. Absolute recall errors increased with set size. This confirmed a clear memory-load effect. The aperiodic exponent was higher during encoding than maintenance, suggesting phase-specific modulation of broadband neural activity during memory formation. Traditional posterior alpha values were more negative during maintenance than encoding. This indicates stronger baseline-relative alpha suppression. However, this encoding-maintenance pattern was much weaker when alpha was estimated as decomposed oscillatory peak amplitude. Overall, the results show that VWM is reflected in both aperiodic and alpha-band dynamics. At the same time, they are also showing that conclusions about alpha modulation depend on how alpha activity is operationalized. This supports a resource-based account, where higher load reduces memory precision.

1. Introduction

Visual working memory (VWM) is the ability to temporarily hold and manipulate visual information. It is supporting ongoing cognition and goal-directed behavior. Through VWM, objects and their features can be kept as internal representations, even when they are no longer present in the environment. However, this capacity is limited. Performance decreases when more items have to be retained, and memory reports become less accurate. Understanding what contributes to this limitation is an important goal of cognitive neuroscience, because VWM is closely related to attention, perception, learning and higher-order cognitive functions.

An important development in VWM research has been the use of continuous-report paradigms. These tasks allow memory performance to be measured on a continuous scale, instead of only through correct or incorrect responses. One commonly used task is the delayed-estimation paradigm, often called the color wheel task. In this task, participants first encode a set of colored items. After a short delay, they report the remembered color of one probed item, using a continuous color wheel. This gives a continuous measure of recall error. Behavioral performance can then be assessed through estimation error, precision and the distribution of responses. The structure of these response distributions is useful, because it helps to distinguish between different theoretical models of VWM.

Several theoretical models have been proposed to explain these limitations. Slot-based accounts describe VWM as limited by a fixed number of discrete storage units, whereas resource-based models propose that a limited representational resource is distributed across remembered items. Variable-precision models further suggest that memory quality can vary across trials and items. In addition, studies of interference and binding show that some errors may reflect structured responses, such as non-target reports or feature misbinding, rather than only random guessing. Together, these models show that VWM limitations can be understood in terms of capacity, precision, noise and interference.

Behavioral paradigms and modelling approaches have improved the understanding of VWM. Still, an important question is how these cognitive-level descriptions are related to neural mechanisms. Electroencephalography (EEG) is useful for this, because it provides millisecond-

level temporal resolution. This makes it possible to distinguish processes such as encoding, maintenance and retrieval in delayed-estimation tasks. Time-frequency analysis is very relevant, because it can be used to examine oscillatory mechanisms that are involved in working memory. Posterior alpha-band activity, usually defined in the 8–12 Hz range, has often been associated with working memory and spatial attention. It has been linked to maintenance of relevant information, suppression of distractors and modulation by memory load. Alpha oscillations have therefore often been interpreted as an electrophysiological marker of working memory maintenance, especially for visual representations that are spatially organized.

One issue in EEG research is both methodological and conceptual. Oscillatory activity and the broadband aperiodic component of the EEG signal are present in the same frequency spectrum. The aperiodic component is often described as 1/f-like activity. It is not treated only as background noise anymore, but also as a meaningful part of neural activity. It has been related to cortical dynamics more generally, including neural population activity, neural gain and excitation-inhibition-related mechanisms.

This becomes important in alpha-band analyses. Changes in alpha-band power may also include changes in the aperiodic background, because oscillatory and aperiodic activity overlap in the frequency domain. Because of this, alpha-band changes should not be considered automatically as changes in oscillatory alpha activity alone. Alpha-band effects are often used to discuss how information is maintained in the brain. Spectral parameterization is useful here, because it separates oscillatory peaks from the aperiodic part of the spectrum and helps with a more careful interpretation of EEG signals.

Some recent studies are pointing to a difference between alpha oscillations and aperiodic activity across working memory phases. Alpha oscillations are usually discussed more in relation to maintenance during the retention period. Aperiodic activity on the other hand, may be more relevant during encoding. This is the phase where sensory information is processed and transformed into memory representations. Because of this, EEG activity should not be treated as one general marker of working memory. Different parts of the EEG signal may relate to different task stages.

This thesis addresses these questions using behavioral and EEG data from a sequential delayed-estimation color wheel task. Participants remembered one, three or five colored items. After this, they reported the color of a probed item using a continuous color wheel. With this design, memory load could be manipulated and recall performance could be assessed through absolute error. It also made it possible to separate the temporal phases of the task, especially encoding and maintenance. Because items were presented sequentially, behavioral and neural measures could also be examined in relation to serial position.

The empirical part is based on 64-channel EEG data, which were analyzed with time-frequency methods and spectral parameterization. Firstly, the analysis was focused on the aperiodic component of the EEG signal, which was indexed by the aperiodic exponent. Another part was focused on posterior alpha activity, and on whether it shows different baseline-relative modulation during encoding and maintenance. Finally, the thesis examines if the phase pattern seen in traditional band-limited alpha estimates is still present when alpha activity is estimated after the oscillatory component was separated from the aperiodic background.

The thesis begins with basic concepts, experimental paradigms and behavioral measures, which are used in visual working memory research. After this, theoretical models of VWM are reviewed. This includes slot-based, resource-based and variable-precision accounts, where the focus is on capacity, precision, noise and interference. The next part moves to neural mechanisms of VWM. Here, the main focus is on EEG time-frequency approaches, posterior alpha-band activity and the distinction between oscillatory and aperiodic components. The empirical part then describes the study conducted in this thesis, including the experimental task, behavioral error analysis, EEG preprocessing, extraction of neural measures for the hypotheses, statistical modelling and results. The thesis concludes by discussing what the findings mean for interpreting oscillatory and aperiodic EEG dynamics in visual working memory.

2. Theoretical Background

2.1 Visual Working Memory: Basic Concepts

This chapter introduces the basic concepts necessary for understanding visual working memory (VWM) as the theoretical basis of the thesis. First, it defines working memory (WM) and VWM, based on key psychological models and it highlights their relevance for explaining short-term maintenance of visual information. The section then outlines the two main experimental paradigms used in VWM research, change detection and continuous report (delayed estimation), and explains how these paradigms enable different types of behavioral measurement. Lastly, the chapter will introduce several common behavioral measures used to assess the performance of VWM, along with an overview of the broader shift within the field from conceptualizing the capacity of VWM as limited to the number of items held in WM toward a more quantifiable approach focused on representational quality.

2.1.1 Definition of working memory and visual working memory

Working memory (WM) is generally described as the system that temporarily holds and manipulates information in a person's mind for a short period of time as just few seconds (Baddeley & Hitch, 1974; Ma et al., 2014). WM supports wide range of cognitive functions including reasoning, comprehension, decision-making and planning actions (Ma et al., 2014; Chai et al., 2018). Unlike long-term memory, which retains information for extended periods of time, WM holds and uses information in an active and easily accessible form (Baddeley & Hitch, 1974; Chai et al., 2018). Thus, WM represents a more than simply a "holding" system, as it is an online processing system with both retention and control components (Chai et al., 2018).

The development of WM theory happened in part due to the limitation of prior theories of Short-Term Memory (STM). STM was historically viewed as a capacity-limited system for briefly storing information, such as a sequence of numbers. This definition failed to account for the fact that numerous cognitive tasks involve manipulating and updating information stored in memory (Chai et al., 2018). As result of the limitations of STM theories, a new theory of WM was proposed

by Baddeley and Hitch (1974). Their multicomponent WM model was explaining that WM consists three interconnected subsystems: (a) the phonological loop, which handles verbal information; (b) the visuospatial sketch pad, which maintains visual and spatial information and (c) the central executive, which directs attentional control and coordinates the various processes involved in WM (Baddeley & Hitch, 1974; Chai et al., 2018).

From a neuroscience perspective, WM has been tied to sustained or persistent neural activity. Historically has been most closely related to fronto-parietal circuits. Mostly to the prefrontal cortex (Chai et al., 2018; Ma et al., 2014). Nevertheless, current views of WM are beginning to suggest that WM representations can be distributed across various parts of the brain. The representation of WM contents can occur through delay-period activity across sensory, parietal and prefrontal regions (Christophel et al., 2017). Furthermore, Christophel et al. (2017) have argued that the distributed nature of WM representations may reflect a hierarchy of abstraction: while sensory areas may maintain more low-level stimulus characteristics, higher-order regions may be more likely to store more abstract, or task-dependent representations.

Visual Working Memory (VWM) is a fundamental component of WM and the primary subject of this thesis. VWM refers to the ability to hold visual object information, such as colors, orientation, and spatial location, in working memory for a brief interval without receiving new sensory input (Bays et al., 2009; van den Berg et al., 2012). According to the Multicomponent WM Framework, VWM corresponds to the function of the Visuospatial Sketch Pad, which is responsible for maintaining visuospatial representations (Baddeley & Hitch, 1974; Chai et al., 2018). VWM is particularly well-suited for experimental study because the visual properties of objects can be controlled and measured with high accuracy (Ma et al., 2014).

A defining feature of VWM is its strong capacity limitation; as the number of items stored simultaneously increases, performance decreases (Ma et al., 2014). Historically, these capacity limitations have primarily been explained in terms of the number of items that could be held in WM (Ma et al., 2014). However, there has recently been a major shift in the field away from a focus on item capacity, towards a greater emphasis on the quality of representations, particularly their precision, as a factor in limiting WM performance (Ma et al., 2014). This shift has made possible the use of Continuous Report paradigms and Computational Modeling techniques to allow

researchers to quantify memory in terms of graded errors and variability (Bays et al., 2009; van den Berg et al., 2012). This view of VWM performance as based on variability and noise in the fidelity of internal representations, shaped by limited resources and interference, is consistent with recent advances in our understanding of VWM (Bays et al., 2009; van den Berg et al., 2012; Ma et al., 2014).

2.1.2 Main experimental paradigms

Visual Working Memory (VWM) has been studied through various experimental paradigms that can systematically manipulate memory load and quantify performance limitations across short retention intervals. The most influential paradigm has been change detection. This paradigm produces a categorical outcome and has often been used to estimate the number of objects that can be maintained (Luck & Vogel, 1997; Pashler, 1988). More recent research increasingly employs continuous report (delayed estimation) paradigms. These allow working memory limitations to be described in terms of representational precision and trial-by-trial variability rather than only capacity of an item (Bays et al., 2009; Ma et al., 2014; van den Berg et al., 2012). Together, these paradigms have contributed to the debate between resource- and slot-based accounts of VWM (Ma et al., 2014; Zhang & Luck, 2008).

2.1.2.1 Change detection

Change Detection Paradigms are generally structured as a sequential comparison task. Participants first look at a sample array of multiple items, then maintain those items in memory for a certain amount of time (the "delay"). In the end they decide if a test array is the same as the sample array or if there is exactly one difference. Performance in this paradigm is generally measured using either the proportion correct (i.e. how often the participants correctly identified a changed item) or derived sensitivity measures, and performance will generally decrease as the set size (number of items) in the sample array increases. The decreasing performance can be used to infer the limits of VWM Storage (Luck & Vogel, 1997; Pashler, 1988).

One of the main advantages of the Change Detection Paradigm is that it has allowed researchers to demonstrate that VWM is capable of storing only a small number of objects. In their seminal study, Luck and Vogel (1997) demonstrated that accuracy remained high for arrays of 1-3 objects,

and declined significantly after ~4 objects. Therefore, Luck and Vogel concluded that VWM capacity is limited to around four integrated object representations (Luck & Vogel, 1997). Furthermore, Luck and Vogel (1997) used change detection to examine whether memory stores individual features or entire objects. They found no significant differences in performance between simple features and multi-feature conjunction objects, indicating that VWM capacity may be limited by the number of objects, rather than the number of individual features. Thus, the change detection paradigm played a pivotal role in developing slot-based capacity frameworks (Ma et al., 2014).

Pashler (1988) further demonstrated that change detection performance is heavily influenced by short-term visual storage constraints and perceptual factors, including masking and inter-stimulus interval. Pashler (1988) specifically demonstrated that change detection performance was affected by an interaction between masking and inter-stimulus interval. That resembles the distinction made by Phillips (1974) between sensory persistence (high performance at very short inter-stimulus interval, but susceptible to masking) and a more durable capacity-limited visual short-term memory (lower performance, but less susceptible to masking at longer inter-stimulus interval) (Pashler, 1988). Additionally, Pashler (1988) demonstrated that familiarity and categorical identity information did little to enhance performance, and thus argued that change detection in this time frame is based primarily on capacity-limited visual memory representations, rather than "identity-location mapping" of familiar objects (Pashler, 1988).

Although change detection has had a large historical influence, it does have a major limitation. Because change detection requires a categorical response, it cannot determine if errors are due to an item being entirely absent from memory, or due to the reduced fidelity/noise in the stored representation (Ma et al., 2014; Zhang & Luck, 2008). This limitation contributed to the shift towards continuous report paradigms (Bays et al., 2009; Ma et al., 2014).

2.1.2.2 Continuous report / delayed estimation

Continuous report paradigms (also known as delayed estimation paradigms) were developed to provide a finer-grain and more quantitative assessment of VWM limitations. In these tasks, participants are presented with a sample array of continuous features (such as colors, orientations),

and then reproduce the feature value of a probed item on a continuous scale (usually through a selection on a color wheel). Unlike change detection, continuous report allows for a complete distribution of estimation errors, which enables the modeling of memory performance in terms of precision, variability, and error sources (Ma et al., 2014; Van Den Berg et al., 2012).

One of the primary contributions of continuous report paradigms is that they show a gradual decline in recall quality as set size increases. Ma et al. (2014) note that recall variability tends to increase continuously with set size in delayed estimation tasks, rather than show a sudden drop-off, which provides a challenge to strong slot interpretations of capacity that are strictly limited by a fixed number of stored items (Ma et al., 2014). This pattern also motivated the development of resource-based conceptualizations of VWM limits (Ma et al., 2014).

Bays et al. (2009) provided strong evidence for the resource view by showing that memory performance declines continuously in continuous report tasks, consistent with the idea of a shared representational resource that is distributed across items. Bays et al. (2009) proposed that when set size increases, fewer resources can be then allocated to each item and that eventually leads to reduced precision. This account supports an opinion that VWM limitations are reflecting degraded representational fidelity under load, rather than an all-or-none storage cutoff (Bays et al., 2009; Ma et al., 2014).

However, continuous report findings have also been incorporated into refined slot-based accounts. Zhang and Luck (2008) proposed that error distributions can be decomposed into a mixture of (a) a distribution of errors around the true target value and (b) a uniform component interpreted as random guessing when the item is not stored (Zhang & Luck, 2008). This approach was used to argue for discrete fixed-resolution representations in VWM, where precision remains relatively stable but the probability of storage decreases when capacity is exceeded (Zhang & Luck, 2008). Importantly, the same continuous report paradigm therefore became central to both sides of the theoretical debate (Ma et al., 2014)

More recently, models have extended the resource framework by proposing that encoding precision is not fixed, even within the same set size. Van Den Berg et al. (2012) proposed the variable precision model, where memory precision fluctuates across items and trials due to

variability in resource allocation. In this view, some trials resemble "guessing," not because nothing is stored, but because the representation can sometimes be extremely noisy (Van Den Berg et al., 2012). This model provides an alternative explanation for the long tails and non-normality of error distributions frequently observed in continuous report tasks (Ma et al., 2014; Van Den Berg et al., 2012).

2.1.3 Key behavioral measures in VWM

Behavioral measures of VWM are determined by the paradigm used to test performance. Both change detection and delayed estimation paradigms have been used to study performance in VWM. Performance has been measured across two different types of paradigms using three key types of measures: accuracy, precision and error distributions (Bays et al., 2009; Luck & Vogel, 1997; Ma et al., 2014; van den Berg et al., 2012; Zhang & Luck, 2008).

2.1.3.1 Accuracy

When a change-detection paradigm is used, performance is usually measured through accuracy. It can be measured also through signal-detection measures such as d' . Participants give a binary response, that is indicating if they detected a change or not (Luck & Vogel, 1997; Pashler, 1988). This type of measure has an important advantage. It provides a clear and easily interpretable estimate of whether visual working memory can support a simple comparison after a short delay. It was also historically influential, because performance decreases as the number of items increases. That was supporting the idea that VWM is strongly capacity-limited (Luck & Vogel, 1997; Ma et al., 2014).

However, accuracy should not be interpreted too directly as a measure of "how much" information is stored. A decrease in accuracy can result from different underlying sources. For instance, the probed item may not have been stored at all, but it may also have been stored in a noisy or degraded form. This makes it difficult to use for a categorical judgment (Ma et al., 2014). In some cases, errors may also arise because the feature is remembered, but assigned to the wrong location, which leads to a misbinding error. Accuracy can show that performance has changed, but it does not specify the mechanism behind this change. For this reason, accuracy is useful as a general summary of performance. But when it is used on its own, it cannot distinguish between competing

accounts of VWM (Zhang & Luck, 2008; Ma et al., 2014). It becomes more informative when it is combined with other measures (e.g., precision, distribution and type of errors).

2.1.3.2 Precision and error distributions

Continuous report (delayed estimation) tasks allow VWM to be described in terms of precision. That means in the fidelity of the stored representation, which is how close the reported value is to the true feature value (Bays et al., 2009; Ma et al., 2014). Precision is important because it matches how we experience memory in real life. Often, we don't completely "forget," but we remember something imperfectly. Methodologically, precision is usually operationalized from the distribution of estimation errors, rather than as a standalone measure.

In continuous report tasks, performance is usually described in terms of the error between the reported and the true feature value. These errors form a distribution, which is often modeled with a Von Mises distribution (circular equivalent of a normal distribution). One important parameter of this distribution is κ . It is commonly used as an estimate of precision. Higher κ values indicate a narrower distribution and therefore more precise memory representations (van den Berg et al., 2012; Ma et al., 2014).

With increasing set size, these error distributions are usually becoming broader. That is suggesting that memory precision decreases when more items have to be maintained (Bays et al., 2009; van den Berg et al., 2012). This finding has been especially important for resource-based models of VWM, because it is consistent with the idea, that a limited representational resource is distributed across items. As more items are encoded, fewer resources are available for each representation, and memory becomes noisier (Bays et al., 2009; Ma et al., 2014).

Importantly, however, precision should not be understood only as a fixed amount of noise present in the memory trace. More recent work suggests that precision is also shaped by how representations change during the delay period. For example, Panichello et al. (2019) showed that memory errors could be reflecting both diffusion-like noise, which causes representations to spread over time, and drift toward stable representational states, or discrete attractors. This drift can reduce random variability by pulling noisy memories toward stable points, but it can also introduce

systematic bias. A narrower response distribution does not necessarily mean that memory is more accurate in every sense.

The most informative output of continuous report tasks is, that it is not only a single precision value, but the full distribution of errors. The error distribution is significant since it can often reveal structure that is hidden when examining only summary statistics (Ma et al., 2014). For example, two conditions could show similar average precision but differ in the frequency of large errors, which is indicating different underlying mechanisms.

To capture this, researchers use modeling approaches to decompose the error distribution into separate components (Ma et al., 2014). A common approach (Zhang & Luck, 2008) assumes responses are a mixture of (a) a target-centered distribution representing noisy but accurate memory and (b) a uniform distribution representing guessing when the item is not stored. Subsequent extensions include swap errors, where participants report a non-target item from the memory array (Bays et al., 2009; van den Berg et al., 2014). This approach is allowing researchers to determine whether performance declines due to increased noise, increased guessing or increased confusions between items.

Importantly, precision is not constant even within the same participant under the same task conditions. Evidence is showing that memory fidelity fluctuates across trials and items (Fougnie et al., 2012). That means, that a single precision parameter can obscure meaningful internal variability. This has motivated models in which precision varies rather than remaining fixed (Fougnie et al., 2012; van den Berg et al., 2012).

Furthermore, error distributions reflect not only random variability but also systematic structure. Panichello et al. (2019) demonstrated that responses can cluster around specific values. It is due to attractor dynamics, which is providing evidence for active stabilization of memory rather than purely passive decay.

2.1.3.3 Behavioral measures and mixture modeling

In continuous report tasks, responses form an error distribution that is reflecting different types of errors. Small errors indicate imprecise but successful memory and large errors can arise either from random responses or from reporting a non-target item.

Mixture models are used to separate these components. In the standard two-component model (Zhang & Luck, 2008), responses are described as a combination of a target-centered distribution (precision) and a uniform distribution (guessing). Extensions include a non-target (swap) component that is capturing confusions between items (Bays et al., 2009). These models provide parameters such as precision and the proportion of different response types.

Importantly, mixture models describe behavioral data but do not completely determine the underlying mechanism. The same error distribution can arise from different underlying processes. That can include discrete item loss, graded variability in precision, interference and misbinding between items (Bays et al., 2009). Mixture model parameters are not process-pure and cannot be uniquely mapped onto a specific memory mechanism. Instead, they can provide a framework for evaluating competing theoretical accounts of VWM (Ma et al., 2014). These measures provide quantitative indices of performance that can be directly related to neural activity.

2.1.4 Summary: from “capacity” to quantitative performance

The two main paradigms used in VWM research have resulted in two separate ways to think about what constitutes memory limitations. The first paradigm, change detection, has traditionally supported the view that VWM is limited in terms of a finite number of objects, and this number is thought to be roughly 4 (Luck & Vogel, 1997; Ma et al., 2014). Slot-based models of VWM support this view as objects are either stored at fixed resolution or are not stored at all when capacity is reached (Zhang & Luck, 2008). The second paradigm, continuous report, has shifted the focus of the field to include a more quantitative measurement of the performance of VWM, in terms of fidelity and variability as a function of load (Bays et al., 2009; Ma et al., 2014; van den Berg et al., 2012). Continuous report methods support a resource based model of VWM performance (Bays et al., 2009; Ma et al., 2014; van den Berg et al., 2012), in which performance is dependent upon the distribution and variability of representational resources. Recent EEG-based

research further supports this movement by showing that behavioral measures of fidelity are associated with unique neural correlates of encoding and maintenance processes (Bender et al., 2025; Ma et al., 2025).

2.2 Models of Visual Working Memory

This chapter examines the formal models developed to account for behavioral limitations of visual working memory. Using the conceptual foundations introduced in Chapter 2, it describes the distinction between measurement models of the behavioral data and models that attempt to interpret the underlying mechanisms. The chapter focuses on slot-based, resource-based and variable precision models.

Building on the behavioral framework outlined before, this chapter examines how the same behavioral patterns can be interpreted differently by competing theoretical accounts of VWM. It focuses on how parameters derived from mixture models are used to support both slot-based and resource-based interpretations, even if there are being based on the same underlying data.

2.2.1 Measurement models and interpretation of behavioral data

Research on visual working memory (VWM) relies on formal models because memory representations cannot be observed directly and must be inferred from behavioral performance. There are various measures of a participant's performance in VWM research, including response accuracy, response variability and full error distributions. Each measure of performance will yield indirect evidence regarding memory representation and organization. However, each measure's interpretation will depend heavily on the specific modeling framework applied to it.

Measurement models are formal frameworks that quantify behavioral performance, but do not specify the cognitive processes that produce the performance. Measurement models are primarily utilized in VWM research utilizing continuous report tasks, where participants reproduce a remembered feature on a continuous scale. The use of a measurement model is exemplified in Zhang and Luck's (2008) mixture model, which characterizes response error distributions as a peaked distribution centered on the target value and a uniform distribution. This model produces estimates of response precision and the proportion of responses categorized as guesses.

However, while measurement models provide a useful summary of performance, these models are generally descriptive rather than mechanistic in nature. That is, the theoretical implications of parameters estimated via measurement models depend on additional theoretical assumptions regarding encoding, storage, and retrieval. For example, Wilken and Ma (2004), Bays et al. (2009), and van den Berg et al. (2012) demonstrated that error distributions produced by measurement models can also be produced through other possible underlying processes, including variability in precision, interference between items, or uncertainty regarding the location of stimuli. Measurement models therefore organize behavioral data but do not uniquely determine the structure of memory.

One of the major issues in the study of VWM has been the tendency to treat parameters estimated from measurement models as direct indices of the underlying mechanisms. For example, within the context of slot-based accounts, the uniform component of a mixture model has typically been interpreted as indicating the proportion of trials in which the probed item was not stored (Zhang & Luck, 2008). However, alternative interpretations demonstrate that similar patterns can emerge even if all items are represented, provided that there is variability in precision across items or trials, or provided that there is imprecision in the binding of feature-locations (Wilken & Ma, 2004; Bays et al., 2009; van den Berg et al., 2012). This demonstrates that behavioral parameters are not mechanism-specific and that many explanations may be consistent with the same data.

2.2.2 Slot-based accounts

Slot-based models suggest that there is a discrete limit on how many objects can be stored at one time in Visual Working Memory (VWM), thus only a few objects can be held in VWM at any given time (Luck & Vogel, 1997; Zhang & Luck, 2008). According to these models, the capacity of VWM is based on the number of “slots” that are available to hold object representations. The primary hypothesis is qualitative in nature: objects are either successfully stored in one of the slots and maintained in relatively high resolution, or the object is not stored in memory, resulting in random guessing (Zhang & Luck, 2008). Therefore, the capacity limits of slot-based models are structural and all-or-nothing, as opposed to accounts that postulate that all items are stored, but with lower levels of precision (Luck & Vogel, 1997; Pashler, 1988; Zhang & Luck, 2008).

2.2.2.1 Core assumptions of discrete storage

Historically, the idea that there is a limited amount of information that we can process at once has been part of more general theories of short-term memory. For example, Miller (1956) proposed that people can keep track of only a few items in short-term memory. Later, Cowan (2001) suggested that when we do not use strategies to organize information, we can usually keep track of around three to five items. Although this work focused mainly on short-term memory more broadly, later research extended this logic to visual working memory. Slot-based models of VWM draw on this line of research and make similar predictions about the number of objects that can be actively maintained, typically around three to four items under normal experimental conditions (Luck & Vogel, 1997; Cowan, 2001; Zhang & Luck, 2008).

Change-detection paradigms provided early empirical support for strong capacity constraints in the visual domain. Pashler (1988) showed that change-detection accuracy did not provide evidence for retention beyond what had been shown in whole-report tasks. He also suggested that the observed limits were not due to categorical identity or perceptual identification failures, but to the characteristics of a restrictive storage mechanism. These findings contributed to the later distinction between weakened representations and the absence of representation.

An important source of evidence for object-based storage is the study by Luck and Vogel (1997), who investigated whether capacity limitations in VWM arise from the number of separate features or from the number of integrated objects. Using a change-detection task, they showed that participants could maintain approximately four colors, four orientations, and approximately four conjunctive objects, such as color plus orientation, without significant additional cost. More importantly, even objects consisting of multiple features were stored as efficiently as single-feature objects. Their results therefore suggested that capacity limitations are based on the number of integrated items, rather than the total number of features. As a result, slot-based models conceptualize VWM storage as a small, fixed set of object-level representations or “slots” (Luck & Vogel, 1997; Zhang & Luck, 2008).

Within this framework, capacity limits are structural: if a display contains more items than available slots, some objects will not be stored (Zhang & Luck, 2008). The key prediction is that

as capacity is exceeded, the proportion of trials in which the probed item was never encoded will increase, while the quality of stored representations will remain relatively stable. Behaviorally, this should appear as an increasing guessing component in response distributions, rather than a gradual increase in noise for all stored items (Luck & Vogel, 1997; Zhang & Luck, 2008). This interpretation is consistent with broader theories suggesting that a small number of discrete units can be maintained concurrently when minimal chunking and long-term memory support are available (Miller, 1956; Cowan, 2001).

2.2.2.2 Mixture-model evidence for storage probability and precision

Zhang and Luck (2008) provided one of the most direct empirical tests of slot-based models. Their paradigm allowed separation of two possible reasons for declining performance as set size increased. First is capacity failure, where some items are not stored and produce guessing responses. Second is precision degradation, where all items are stored but become noisier. Slot-based models predict the first pattern and resource-based accounts predict the second. To distinguish between these possibilities, Zhang and Luck (2008) used a continuous-report paradigm. There, participants selected the remembered color of a probed item from a color wheel.

This paradigm generated a complete distribution of recall errors instead of only a binary correct and incorrect response. Zhang and Luck (2008) proposed that responses arise from a mixture of two trial types. When the probed item is successfully stored, responses cluster around the correct value. When the item is not stored, responses are uniformly distributed across the color space, which is reflecting guessing. They modeled memory-based responses with a von Mises distribution and guessed responses with a uniform distribution. This allowed them to estimate two parameters. First is P_m , which is the probability, that the probed item was stored in memory. Second is SD , which is the precision of stored representations. If capacity limits reflect discrete storage slots, increasing set size should reduce P_m and have little effect on SD . In contrast, resource-based theories would predict a systematic increase in SD as memory load increases.

In their first experiment, Zhang and Luck (2008) were testing arrays of three or six colored squares. Precision did not vary significantly across set sizes, which is consistent with a slot-based account. Storage probability dropped strongly at the larger set size. That means that increasing

memory load reduced the likelihood that an item was stored, but did not measurably reduce the quality of the representations that were stored. These results supported the interpretation, that only a subset of items was retained in memory, while the remaining items failed to be stored and produced guessing responses (Luck & Vogel, 1997; Zhang & Luck, 2008). Control analyses further suggested that this dissociation was not explained by insufficient encoding time, perceptual limitations or categorical encoding of colors.

Zhang and Luck (2008) also examined how slots could be allocated below capacity. They proposed a hybrid version of slot-based storage. There, fixed number of objects can be stored, but unused slots can improve the precision of stored items when set size is low. In this “slots-plus-averaging” account, one object can occupy more than one slot when fewer objects are presented than the available number of slots. Their results showed, that memory precision decreased from set size 1 to 3, but then remained quite stable between set sizes 3 and 6. Storage probability showed a shallow decline below capacity, which was followed by a sharper drop when capacity was exceeded. This pattern is suggesting two modes of operation. First is model below capacity, where most items are stored and precision can vary depending on how many slots are assigned to each item. Second is model above capacity, where additional items increasingly fail to be stored.

The same study also looked at attentional priority and limitations on memory consolidation. Attentional priority greatly affected the likelihood that cued items would be placed into memory, but it had no real impact on the accuracy of the information that was stored. Similar to the effects found in backward masking, attention had no effect on the precision of items once they entered memory, as long as the stimulus-mask interval was small enough. Therefore, these data suggest that attention and memory consolidation primarily determine if an item will enter memory, not the level of detail about the item in memory (Zhang & Luck, 2008).

In addition to assessing whether the same patterns could generalize beyond color memory by utilizing stimuli varying continuously along a shape dimension. The results demonstrated a pattern identical to those found with color. That is, storage probability declined as set-size increased; whereas, precision was relatively stable across larger set-sizes. Together with the data from the cueing/masking studies, this suggests that the proposed limit is related to how many objects become and remain in memory; rather than representing a specific type of feature or a gradual

degradation of all stored representations. This interpretation provides the theoretical starting point for resource-based and variable-precision accounts, that are discussed in the next section.

2.2.3 Resource-based and variable precision accounts

A slot-based model provides an important representation of Visual Working Memory (VWM) capacity as providing a fixed number of slots where a relative high level of stability of resolution is maintained. An important implication of this view is that there will be little or no relationship between set size and memory precision until the capacity limit is reached. The decrease in performance observed at larger set sizes would result from the increase likelihood of the item being probed not being held in memory (Luck & Vogel, 1997; Zhang & Luck, 2008). However, recent empirical data has challenged this view, and it appears that representational accuracy tends to decrease continuously with increasing set size as opposed to remaining constant until a certain point of maximum set size is reached.

Alvarez and Cavanagh (2004) demonstrated that change detection performance is a direct function of the stimulus complexity: Even at very low set sizes, stimuli with greater information content may lead to poor performance. Similarly, signal detection theory (SDT) analyses also support the view that change detection performance can be accounted for by a continuous noise-limited system where the discriminability of two items decreases as the internal noise increases with the load (Wilken & Ma, 2004; Macmillan & Creelman, 1991).

The use of continuous-report paradigms provides further support for this interpretation by allowing researchers to measure precision directly. Across multiple studies, researchers have found that the variability of recall increases continuously with the set size rather than suddenly at some presumed capacity limit (Wilken & Ma, 2004; Bays & Husain, 2008). Bays and Husain (2008) found, for example, that recall variance increases monotonically with load, including within the range of set sizes traditionally considered to be less than the slot-capacity limit.

Finally, there is evidence from research concerning the role of attentional allocation and interference. Awh, Barton, and Vogel (2007) showed that many apparent capacity effects can be attributed to encoding conditions and competition among items rather than a strict structural

bottleneck. When encoding conditions are optimized, performance can exceed classic capacity limits.

Decreases in performance with increasing load appear to reflect an increase in noise, an increase in interference, and a reduction in the signal to noise ratio of the memory trace, rather than an increase in the number of items lost. Resource-based models were developed to formalize this perspective and proposed that VWM capacity represents a limited but continuous resource that can be allocated to multiple items (Bays & Husain, 2008; Wilken & Ma, 2004). As the number of items stored increases, each item receives a decreasing share of this resource resulting in a decreasing representational precision and a gradual decline in performance. This re-conceptualization of capacity as representational fidelity rather than probability of storage constitutes the basis of the formal models that are discussed in the next section.

2.2.3.1 Shared Resource and Flexible Precision Accounts

Resource-based models suggest a fundamentally new structure of visual working memory (VWM) compared to slot-based models. Resource-based models assume there exists a single, shared representational resource which can be used to represent any or all items. The degree of precision of each item's representation is determined by how much of the available representational resource is allocated to it; thus, larger set sizes result in decreased precision per item (Wilken & Ma, 2004; Bays & Husain, 2008; Ma et al., 2014).

In this type of model, all items are thought to exist in memory, but their representations become progressively less precise as set size increases. Therefore, the primary source of performance limitations associated with resource-based models arises from increased representational noise rather than discrete failures of memory. Resource-based accounts view capacity limits as an outcome of signal-to-noise ratios governing representational fidelity, rather than structural limits on the number of objects that can be stored in memory.

The fundamental assumption of resource-based models is that VWM utilizes a limited pool of representational resources that can be distributed among any or all items in memory (Wilken & Ma, 2004; Bays & Husain, 2008). Memory precision is directly related to the relative amount of representational resource allocated to an item. If only one item is being maintained, it can be

represented with high fidelity. If multiple items are being held in memory, each item must share the available resources and is represented with decreasing precision as set size increases.

It is also important to note that these models do not posit a qualitative difference between the memory representations of stored and un-stored items. Rather, behavioral errors are believed to arise from noise in the representation of an item, rather than guessing due to loss of the item. Very low-fidelity representations may appear behaviorally equivalent to guessing, but should be viewed as weak representations rather than as a lack of information about the item (Wilken & Ma, 2004).

Signal Detection Theory (SDT) has provided a formal basis for interpreting resource-based models. Wilken and Ma (2004) demonstrated that what has traditionally been viewed as evidence of fixed-capacity limits based on change detection performance can be alternatively accounted for as changes in discriminability resulting from increasing internal variability, rather than as failures to store items (Wilken & Ma, 2004; MacMillan & Creelman, 1991). Thus, capacity limits in resource-based models arise as emergent properties of representational noise and decision processes, rather than as discrete storage boundaries.

Some early versions of resource-based models assumed that all items would receive an equal amount of representational resources, and thus predicted uniform and monotonically decreasing precision as set size increased. More recent versions incorporated flexible precision, where resource allocation is variable both across items and across trials (Bays & Husain, 2008). Some items may therefore receive higher precision than other items encoded at the same set size. Flexible-precision models can account for variation in fidelity seen in continuous-report tasks, and provide an alternative to discrete-guessing explanations for varied error distributions.

Instead of viewing changes in accuracy with set size as evidence for lost items, flexible-precision models view those changes as reflecting variability in resource allocation and representational uncertainty. Thus, precision becomes a naturally stochastic property of memory representations, and confidence and fidelity can vary continuously rather than discretely (Bays & Husain, 2008).

The differences between slot-based and resource-based approaches can be described in terms of qualitative storage limits versus graded uncertainty. Slot-based approaches describe items as either stored or not stored, with failure based on an item's absence (Luck & Vogel, 1997; Zhang & Luck,

2008). Resource-based models assume that all items have some level of representation, but the degree of representation varies depending on the amount of resources assigned to each item (Bays & Husain, 2008; Wilken & Ma, 2004). Therefore, capacity can be described either as a limited number of stored objects or as a limited signal-to-noise ratio determining representational fidelity.

By framing capacity limits as constraints on representational precision, resource-based and flexible-precision accounts align VWM with broader principles of neural coding and probabilistic representation (Ma et al., 2014). However, these models also create an important question: how should near-uniform error distributions at high set sizes be interpreted? One possible answer is that they reflect actual item loss. Another is that they represent the extreme end of a precision distribution, where an item is stored so poorly that responses look almost random. This uncertainty has motivated variable-precision and hybrid models, which are discussed in the next section.

2.2.3.2 Bays et al. (2009): Shared Resource with Non-Target Responses

As part of the ongoing debate over slots vs resources, the delayed estimation paradigm has become a key test bed for investigating full recall error distributions, as opposed to simply reporting binary correct/incorrect judgments (Ma & Wilken, 2004; Luck & Zhang, 2008). Zhang and Luck (2008) proposed that the error distributions found in delayed estimation paradigms represent a mixture of two fundamentally different types of responses: memory-based reports centered around the actual target value, and random guesses that are uniformly distributed. In essence, Zhang and Luck (2008) suggested that increases in set size lead to an increase in the likelihood that the probed item did not get stored, thereby increasing the proportion of the uniform component.

Bays et al. (2009) accepted the experimental utility of the continuous report paradigm, but rejected the theoretical interpretation of Zhang and Luck (2008). In addition to recalling the feature value associated with each item, participants must also select the correct item at test, most commonly based on its spatial location. The uncertainty introduced by this second retrieval demand regarding both location and feature-location correspondence can result in very high levels of error, even when many items have been successfully stored. The noise generated in this selection process can lead to systematic non-target reports, rather than truly random guesses (Bays et al., 2009).

If a significant proportion of the errors represented in the long-tail of the distribution represents incorrect retrieval of the stored item, then a uniform-looking tail is no longer uniquely indicative of discrete limits to storage capacity. In the typical delayed estimation method, successful completion requires encoding not just feature values, but also enough information about spatial location and feature-location associations to select the correct internal representation (Wilken & Ma, 2004; Bays et al., 2009). Bays et al. (2009) therefore contended that there is no direct relationship between the uniform error component and storage failure.

Even if many colors are encoded with good accuracy, failure to accurately encode spatial location or feature-binding can cause the observer to report the color of a non-target item. When non-target-centered responses are computed relative to the actual target, they can generate long tails which are approximately uniformly distributed over time (Bays et al., 2009; Zhang & Luck, 2008). Bays et al. (2009) developed a diagnostic test for distinguishing these possibilities and demonstrated that non-target clustering was reliably observed and increased with set size, suggesting that many large errors reflected reports of non-targets rather than simply random guesses.

In order to express their criticism of the two-component mixture model, Bays et al. (2009) developed a three-component error model. This model includes a target-centered component describing variance in memory for the examined feature, a non-target-centered component, and a uniform component representing truly random guesses that do not relate to the previously stored items (Bays et al., 2009). The two-component model considers large deviations from the target to be guesses because it does not systematically treat responses to non-targets. In contrast, the three-component model distinguishes between true random responding and retrieval of the wrong item from memory.

Once non-target responses were modelled explicitly, the remaining uniform component was much smaller than the “guessing rate” reported when using a two-component analysis (Bays et al., 2009; Zhang & Luck, 2008). Furthermore, the proportion of non-target responses reliably increased as set size increased (Bays & Husain, 2008; Bays et al., 2009). Therefore, the “guess rate” parameter obtained from a two-component model is not process-pure, because it confounds true guessing with non-target responses that arise from spatial or binding uncertainty (Bays et al., 2009).

An important contribution made by Bays et al. (2009) is the separation of load-related degradation from encoding limitations. Slot-based theories would suggest that once set size exceeds capacity, items fail to be stored and guessing sharply increases (Zhang & Luck, 2008). However, increasing set size had no significant impact on the uniform guessing portion, but resulted in lower precision and higher non-target responses. In contrast, increasingly brief exposures led to an increase in truly random guesses, while longer exposure times reduced the uniform guessing component (Bays et al., 2009).

This dissociation suggests that part of what can appear as “guessing” may be due to failures in encoding rather than structural storage limitations. Guessing rates are influenced by encoding conditions and cannot be used as a direct measure of capacity (Bays et al., 2009; Wilken & Ma, 2004). Therefore, a decrease in performance is better interpreted as an increase in representational noise, spatial or binding uncertainty, and confusability with increasing load, rather than as direct evidence that items were not stored.

2.2.4 Summary: why noise / interference / variable precision matter

This chapter examined the main issue in the slot versus resource debate: do performance declines indicate discrete item loss or gradual changes in representational quality?

Slot-based models view capacity as a constant number of object representations, and predict that when the number of objects exceeds this fixed number, some objects are not retained in memory and later result in guessing (Luck & Vogel, 1997; Zhang & Luck, 2008). Resource-based and variable-precision models, however, show that the same behavioral signs - set size effects, flat error tails, and apparently random guessing - can arise from increased noise, interference, and variability in precision, while still maintaining representation of all items (Wilken & Ma, 2004; Bays & Husain, 2008; van den Berg et al., 2012).

Bays et al. (2009) further demonstrate that a large proportion of errors classified as "guessing" in two component mixture models can be accounted for by interference among the stored items, especially spatial binding errors which result in non-target responses. When these types of error are specifically modeled, the residual rate of truly random responding remains relatively low,

regardless of set size. This finding reduces claims that uniform error terms provide direct evidence for discrete storage failures.

Variable-precision models continue in this way of reasoning by letting representational quality vary randomly between items and trials (van den Berg et al., 2012). In this model, very poor-precision representations can produce responses that are statistically equivalent to random guessing, even though there is a memory trace present. Therefore, guessing-like behavior is not necessarily indicative of an item being never stored, but could be related to random variability in neural gain, attentional distribution, or encoding fidelity.

Collectively, the models described in this chapter illustrate that mixture-model parameters are not theoretically predictive of a particular memory architecture. The above modeling framework provides the theoretical underpinnings for the next part of this thesis, where this viewpoint will be applied to electrophysiology, specifically alpha oscillations and aperiodic activity, as potential neural indices of precision, noise and interference in visual working memory.

2.3 Neural Mechanisms of Visual Working Memory

The previous chapters were examining the behavioral aspects of VWM and focused on how limitations of performance are expressed and modeled. This chapter examines those limitations at the neural level through focusing on the temporal dynamics of neural activity associated with VWM processing.

A key methodological distinction is between phase-locked and induced neural activity. Phase-locked activity occurs with relatively consistent timing and phase across trials, which means that it is preserved in averaged event-related potentials (ERPs). Induced activity, however, is more variable from trial to trial, either in timing or phase, and may therefore be weakened or lost during averaging. Consequently, ERP analyses capture only part of the neural activity contained in the EEG signal (Morales & Bowers, 2022). Time-frequency analysis addresses this limitation by examining changes in neural activity across both time and frequency, allowing the study of both phase-locked and non-phase-locked (induced) activity.

EEG provides millisecond-level temporal resolution and is well-suited for studying the encoding, maintenance and retrieval phases of VWM (Kim, 2019). However, traditional EEG analysis methods have limitations. ERP approaches require activity to be time-locked to events, while Fourier-based methods capture frequency information but lose temporal dynamics. As a result, neither approach alone fully captures neural activity.

2.3.1 Neural accounts of visual working memory

Research on visual working memory (VWM) has progressed across multiple levels of explanation, from behavioral measures of performance and computational modeling of constraints on capacity, precision, and variability to the examination of underlying neural mechanisms. Previous chapters discussed behavioral paradigms and formal models of constraints on performance and represented competitive representational architectures. While behavioral data provide evidence about the nature of the constraints on performance and can be used to specify competing representational architectures, it does not indicate how those constraints are embodied in neural circuitry. To answer this question, it is necessary to use methods that provide access to the neural dynamics of cognitive processes as they occur over time (Trutti et al., 2021).

EEG has bridged the gap between cognition and brain function by allowing the measurement of neural activity during encoding, maintenance, and retrieval. Early EEG studies relied on ERP-based methods to examine neural responses that are time-locked to task events, supporting the view that working memory involves active maintenance (Luck & Vogel, 2013). However, ERP analyses selectively capture phase-locked activity and may miss neural dynamics that vary across trials.

More recently, the use of time-frequency analysis has allowed researchers to study neural oscillations over time. Time-frequency analysis has identified that working memory tasks are associated with not only time-locked activity, but with induced oscillatory activity. Induced oscillatory activity is indicative of top-down attentional control, spatial coding, and maintenance. Alpha-band activity has consistently been associated with working memory function.

Additionally, there has been an increase in the recognition that the traditional band-limited power measures of the EEG signal do not represent pure oscillatory activity. Rather than representing

only oscillatory activity, the EEG signal represents both periodic (oscillatory) and aperiodic (1/f-like) components. Aperiodic components contribute to the total power in the frequency spectrum and can affect the estimation of oscillatory power. Therefore, separating the aperiodic and periodic components is necessary to accurately interpret the oscillatory activity (Brake et al., 2024).

2.3.1.1 Persistent neural activity as a classical account

Early research on the neural basis of working memory provided one of the first and most influential accounts of how information is stored using sustained neural activity. The classical view posits that once a neuron fires to encode task relevant information, those same neurons will continue to fire during the delay period of a working memory task until the stimuli are again presented. Therefore, sustained activity is thought of as more than just a correlation of memory; it is considered the actual substrate upon which the memory exists.

Much of the empirical evidence supporting the persistent activity theory of working memory comes from single unit recordings in non-human primates performing delayed response tasks. Fuster and Alexander (1971), demonstrated that neurons in the prefrontal cortex will begin to fire when a non-human primate sees a cue and then continue to fire throughout the delay period. Since these neurons continued to fire without receiving any additional sensory cues and before any motor responses occur, they were assumed to represent the temporal retention of the cue rather than the processing of that cue or the planning of an appropriate motor response. This work was later incorporated by Goldman-Rakic (1995) into comprehensive model of working memory, which posited that working memory is based on prefrontal neurons that exhibit stimulus specific delay activity. According to Goldman-Rakic's model, repeated excitatory connections between neurons is stabilizing firing patterns and allowing information to be maintained for extended periods of time.

Evidence supporting this theory also came from functional magnetic resonance imaging (fMRI) studies, that were conducted in humans. fMRI studies have consistently reported increased BOLD signal in the frontal and parietal lobes during the delay period of working memory tasks. Moreover, studies have shown that the magnitude of the BOLD signal increases with the amount of information that must be held in working memory. Similar reasoning has been used to interpret

EEG data. Components present during the delay period of working memory tasks were often interpreted as evidence that working memory storage relies on sustained activation of neural populations. A prominent example of this is the contralateral delay activity (CDA), which is discussed in more detail in the upcoming section. If neurons keep firing in the process of remembering information, it follows that the firing itself will be the memory trace. Therefore, persistent neural firing provided a way to relate theoretical accounts of working memory to actual neural processes (Goldman-Rakic, 1995).

However, there were growing concerns with the sustainability of the original theory. First, sustained firing consumes metabolic resources, and therefore raises questions about its effectiveness at high load levels or during longer retention periods. Second, behavioral and computational studies have shown that the precision of memory is continuously dependent upon the number of items being held in memory, and their relative importance (Bays et al., 2011; Ma, Husain, & Bays, 2014), which suggests that working memory involves resource sharing rather than maintaining fixed representations across all items.

The electrophysiology literature has been even less supportive of the original theory than behavioral/computational results. While some neurons do fire persistently throughout the delay period, many other neurons fire in a manner that is transient, dynamic or variable over time. In addition, the information that is encoded about the stimulus being remembered is often accessible via decoding of the population activity even though the average firing rate of those cells has not increased (Sreenivasan, Curtis, & D'Esposito, 2014; D'Esposito & Postle, 2015). Therefore, representing working memory via persistent firing of single neurons is not necessary, and is likely insufficient.

2.3.1.2 Contralateral Delay Activity (CDA)

The contralateral delay activity (CDA) is an event related potential (ERP) and one of the most widely used electrophysiological markers of the maintenance of visual working memory (VWM) in EEG studies. The CDA is a sustained, negative-going ERP observed over posterior parietal and lateral occipital regions contralateral to the visual hemisphere where information is being actively

maintained. The CDA emerges about 200–300 ms post-stimulus onset and continues until the end of the delay period.

Initially, the CDA was identified by Vogel and Machizawa (2004) using a laterality-based change detection paradigm designed to separate neural activity associated with the storage of information from other types of sensory or general task-related activity. Participants were told to remember information that appeared on one side of the visual field while ignoring information on the opposite side.

One of the defining features of the CDA is its sensitivity to memory load. The amplitude of the CDA increases as the number of items being maintained in visual working memory increases, but only until a clearly asymptotic limit is reached (Vogel & Machizawa, 2004). CDA amplitude does not continue to increase as memory load increases beyond an individual's capacity, even though task difficulty increases. Furthermore, the strong contralateral specificity of the signal supports the idea that the CDA indexes spatially organized maintenance processes in posterior cortical regions.

CDA can also be used to identify individual differences in working memory capacity and attentional control. Vogel et al. (2005) demonstrated that CDA amplitude reflects not only how many items are stored, but also how efficiently capacity is utilized. Together, these results indicate that individual differences in VWM performance reflect both storage limits and the efficiency with which irrelevant information is filtered from the storage process. Consequently, the CDA has become a critical tool for connecting behavioral estimates of capacity with underlying neural control mechanisms (Luck & Vogel, 2013).

Although the CDA is a robust electrophysiological measure of VWM maintenance, it is not without functional ambiguity. A primary concern is whether the CDA mainly reflects the number of object representations stored, or more broadly indexes attentional selection processes that determine which objects enter a limited-capacity store. Methodologically, because the CDA is derived from averaging ERPs, it captures activity that is time-locked and phase-consistent across trials. Therefore, the CDA is less sensitive to induced or non-phase-locked oscillatory activity that may also be involved in working memory maintenance.

2.3.1.3 From sustained signals to dynamic neural processes

Previous chapters provide a view on how the theoretical views on the neural basis of working memory maintenance have developed. Initially, early neural models focused on the idea of maintained neural activity, later EEG studies found stable event-related markers like the contralateral delay activity. In addition to providing a better understanding of working memory, these perspectives show that there are significant limitations in traditional ways of analyzing neural data.

One common feature of many studies supporting persistent activity and CDA-based views is the use of time-locked averaging and discrete event-related analyses. Since both of these methods involve the alignment of neural signals with specific events in time (e.g., stimulus onset or delay periods) and then the averaging of signals from each of those aligned times across all trials, these approaches tend to emphasize signals that appear stable and continuous over time. Such averaging can conceal substantial variability in neural signals and create the illusion of sustained neural signals, even if the actual neural signals are temporally structured and/or intermittent (Luck, 2014; Cohen, 2014).

These same limitations can be applied to ERP-based measures of the CDA. Although the CDA has been an extremely influential EEG marker of visual working memory maintenance, it represents the activity that is phase-locked to the stimulus events and is consistent across trials. Because of this characteristic, ERP analyses are generally less sensitive to neural processes that are not directly locked to the stimulus events (i.e., not phase-locked), which includes oscillatory activity that varies in both amplitude and timing across trials (Luck & Vogel, 2013; Cohen, 2014).

Such continuous temporal dynamics are not typically captured through methodologies that only examine average activity during predetermined task intervals. Therefore, new methodologies are required to study such temporal dynamics. Analytical tools that allow researchers to analyze neural activity as a function of time while differentiating among different frequency components of the signal are necessary. Time-frequency EEG analysis allows researchers to accomplish this goal, because it permits the examination of oscillatory activity as it develops during encoding, delay, and retrieval phases (Cohen, 2014).

This methodology enables investigators to determine how changes in different frequency bands over time relate to working memory demands and control processes. Rather than replace prior EEG markers, time-frequency analysis complements prior EEG markers by indicating neural dynamics that are not observable in averaged time-domain signals. Therefore, the next section will introduce time-frequency EEG methodology and explain why time-frequency analysis is particularly well-suited for examining the neural basis of visual working memory.

2.3.2 Time-frequency EEG approaches to working memory

Research using only traditional time-domain EEG measures (e.g. ERP) to examine visual working memory has provided limited information regarding how neural activity develops across both time and frequency. The use of time-frequency analysis allows researchers to gain a much greater understanding of the spectral development of neural activity throughout a trial. This method offers an alternative perspective on the cognitive dynamics that take place during working memory tasks.

2.3.2.1 Why oscillations matter for cognition

To understand the neural basis of visual working memory (VWM), it is important to use methods that can capture not only where information is represented in the brain but also how neural activity is organized and coordinated over time. Early models were emphasizing sustained neural signals but new evidence suggests, that cognitive processes (e.g. attention and working memory), rely on dynamic patterns of neural activity, that is distributed across brain networks (Christophel et al., 2017; Miller et al., 2018).

Neural oscillations offer a way to study these dynamics by reflecting coordinated fluctuations in neural excitability at the population level. Oscillatory activity is increasingly interpreted as a mechanism, that is supporting communication, coordination and control among neural systems, rather than directly encoding stimulus content (Miller et al., 2018; Schmidt et al., 2023).

One important role, that is attributed to oscillations, is the ability to regulate the communication between brain regions. Working memory representations are distributed across sensory, parietal and prefrontal areas. This distribution requires coordinated activity across these regions.

Oscillatory dynamics can provide a mechanism for the coordination through the temporal alignment of neural excitability (Christophel et al., 2017; Miller et al., 2018).

Importantly, analyzing neural activity in the frequency domain can reveal temporal structure that is not captured by time-locked measures alone. This is very relevant for working memory, where neural activity during encoding, maintenance and retrieval unfolds dynamically over time (Kim, 2019).

It is important to distinguish oscillatory activity from non-oscillatory components of neural signals. The EEG power spectrum reflects both periodic and aperiodic components, each of which can be carrying functionally relevant information (Brake et al., 2024). This distinction further motivates the use of time-frequency approaches to obtain a more complete characterization of neural activity during working memory tasks.

2.3.3 Alpha-band oscillations in visual working memory

Alpha band activity has emerged as a major area of study using EEG regarding visual working memory (VWM), because it appears to be a way to see how internally generated representations are selectively controlled and used in memory tasks. Instead of being one mechanism, alpha-band activity has been associated with multiple overlapping functions. The next sections will review each of these interpretations in order, starting with spatial coding, then lateralization effects, inhibitory control, and finally, the effect of memory load on alpha-band activity.

2.3.3.1 Alpha oscillations and spatial coding

Alpha oscillations have been most directly linked to VWM in tasks that require people to maintain spatial information. In studies using both EEG and MEG, changes in posterior alpha-band activity are often observed when participants have to remember spatial locations. Because this association has been found quite consistently, alpha-band activity has been suggested to play a role in maintaining spatial representations during the delay period of VWM tasks (Pavlov & Kotchoubey, 2022; Wianda & Ross, 2019).

Further evidence for this relationship comes from studies showing that posterior alpha activity reflects the spatial properties of the remembered stimuli. In particular, alpha power over occipitoparietal regions appears to contain information about the spatial location of items held in memory. This suggests that spatial coding may be one important organizing feature of VWM representations (Bender et al., 2025).

This pattern also fits with the retinotopic organization of the visual cortex. Alpha-band activity recorded over posterior scalp sites often varies according to the visual field location of the remembered items (Christophel et al., 2017; Kim, 2019).

More direct evidence for alpha-based spatial coding has also come from multivariate decoding studies, which have shown that spatial information can be decoded from patterns of alpha-band activity (Bender et al., 2025). In addition, the researchers separated actual oscillatory alpha-band activity from non-oscillatory components of the EEG, and found that decoding performance was significantly better for oscillatory alpha-power compared to total alpha-power. Therefore, the results support the idea that the actual alpha oscillations carry spatial information during the VWM maintenance phase, rather than just overall broadband spectral changes (Bender et al., 2025).

In this view, alpha oscillation patterns represent how neural resources are allocated to different parts of the retina thus creating a map of which parts of the visual field are most relevant and which are less so (Pavlov & Kotchoubey, 2022).

More recent research has refined this interpretation by showing that posterior alpha-band activity is not a singular phenomenon. Rodriguez-Larios et al. (2022) demonstrated that during VWM tasks, at least two distinct posterior alpha-band activities exist. These findings suggest, that spatial coding in VWM relies on the interaction of multiple alpha-generators and not only on a single homogeneous oscillatory process.

2.3.3.2 Alpha as inhibition and top-down control

An important interpretation of alpha-band oscillations proposes that alpha activity reflects a mechanism of functional inhibition. Rather than indexing resting state or disengagement, increases in alpha power are thought to reduce cortical excitability in a goal-directed manner, thereby

limiting the processing of information that is currently irrelevant (Wianda & Ross, 2019; Manza et al., 2014). Electrophysiological and neuroimaging studies provide evidence supporting this model through the demonstration of inverse relationships between alpha power and neuronal spiking and alpha power and behavioral sensitivity. For example, within working memory (WM) the functional inhibition of WM representations is critical due to the need to maintain these representations while preventing them from being disrupted by incoming sensory input or competing mnemonic activity (Sreenivasan et al., 2014).

There is strong evidence that alpha power increases in working memory retention intervals where external input is either irrelevant or could be disruptive (e.g., Wianda & Ross, 2019; Jensen et al., 2002; Bonnefond & Jensen, 2012). However, alpha power can also decrease during retention, especially in experiments without distractors. This alpha desynchronization is generally interpreted as reflecting active maintenance and attentional prioritization of the stored information (Erickson et al., 2019). When a cortical region is recruited to hold or manipulate memory content, its alpha power decreases. That is indicating increased neuronal excitability and allowing the information to be actively processed (Wianda & Ross, 2019; Magosso & Borra, 2024). These results indicate that alpha activity is used to actively control the processing of relevant versus irrelevant information rather than passively disengaging from the processing of irrelevant information. Additionally, in situations where there is a need to filter out distracting information stronger alpha activity has been found to predict better performance in resisting distractions and maintaining memory stability (Manza et al., 2014). Furthermore, alpha activity may increase prior to the onset of anticipated distractors, suggesting that alpha-mediated inhibition is proactive and provides a protective mechanism for the maintenance of WM representations (Wianda & Ross, 2019; Bonnefond & Jensen, 2012).

The proposed inhibitory account of alpha oscillation closely parallels the mechanisms of attentional gating (Manza et al., 2014; Wianda & Ross, 2019). As such, alpha oscillations serve as a regulatory mechanism controlling the flow of processing resources to allow for the continued stability of internally maintained representations during the delay period. That is, when attention is directed towards external stimuli, alpha power decreases in areas of the brain responsible for processing those stimuli, whereas directing attention internally during retention is associated with

increases in alpha power that help suppress the processing of incoming sensory input (Wianda & Ross, 2019; Manza et al., 2014; Sreenivasan et al., 2014).

Theoretical frameworks of cognitive control further support this interpretation. Sreenivasan et al. (2014) propose that working memory maintenance arises from dynamic interactions between sensory representations and higher-order control systems rather than from sustained activity within a single region. Alpha oscillations provide a plausible neural mechanism for implementing this bias by regulating cortical excitability during maintenance. In the context of such a model, alpha activity should be viewed as a mechanism that facilitates the control processes involved in selecting which representations will be maintained or suppressed, rather than serving directly as a storage mechanism.

Together, there is convergent evidence to support the notion that alpha oscillations serve as a neural mechanism of inhibitory control that underlies top-down control in working memory and enables the selective maintenance of internal representations while minimizing the impact of competing inputs (Manza et al., 2014; Wianda & Ross, 2019; Sreenivasan et al., 2014; Miller et al., 2018).

2.3.3.3 Alpha and memory load

One of the most supported empirical findings across the Visual Working Memory (VWM) literature is that the alpha band's activity is consistently modulated by memory load. From studies using both EEG and MEG technologies, there exists a consistent relationship between the posterior alpha band's power during the delay phase and the number of items an individual maintains in their working memory. However, the nature and interpretation of these load-dependent effects are still somewhat ambiguous (Wianda & Ross, 2019; Pavlov & Kotchoubey, 2022).

Many studies have reported a relationship between the alpha band's power and increasing set size, such that as set size increases, alpha power either decreases at a slower rate or increases relative to lower-load conditions (Wianda & Ross, 2019). Such results are typically interpreted as indicating an increase in the demands placed upon an individual's top-down control processes as they attempt to stabilize internal representations of stimuli as the number of stimuli in memory increases. On the other hand, computational modeling has suggested that as the number of items maintained within working memory increases, the amount of alpha/beta activity will decrease as

neural networks move from a rest state into a more active state where they begin to actively represent the stimuli being held in memory (Lundqvist et al., 2011).

Alpha load-dependent activity has also been related to individual differences in working memory capacity. Subsequent research has shown that these individual differences are due to factors beyond those associated with simply maintaining a greater number of items within working memory, such as filtering out irrelevant information and controlling access to memory (Vogel et al., 2005). These findings suggest that alpha-band activity is not a simple reflection of a single capacity parameter but instead represents multiple interacting processes involved in tasks requiring working memory.

Traditional frequency-time analysis techniques fail to differentiate between the periodic oscillations and the broad band non-periodic, 1/f-like activity/background of the EEG spectrum, which means that any observed changes in alpha power can include contributions from changes in the background signal. In contrast, Liu et al. (2025) demonstrated that when the oscillatory alpha activity and aperiodic components are separated, increases in alpha power are clearly associated with an increase in target load compared to traditional methods. The aperiodic exponent on the other hand appears to be independently influenced by both target load and distractor load, indicating that memory load affects two separate spectral components through differing neurophysiological mechanisms. Bender et al. (2025) found similar results, demonstrating that oscillatory alpha activity and aperiodic dynamics contain different information during working memory tasks.

2.3.4 Aperiodic activity and its functional meaning

Recent advancements in EEG analysis show that in addition to oscillations, there are broadband non-oscillatory dynamics present in neural power spectra. Aperiodic dynamics were previously treated as "noise," however, recent research has shown that aperiodic dynamics represent real and meaningful characteristics of the neural activity of the brain.

2.3.4.1 Periodic vs. aperiodic components of the EEG signal

EEG signals contain multiple spectral components that reflect various aspects of population activity in the brain. When describing the spectral components of EEG in the frequency domain, these components are typically identified as either periodic (oscillatory) or aperiodic (1/f-like) activity. Both types of components exist simultaneously within the same EEG recording, therefore, it is critical to understand that the power spectrum of EEG represents a combination of both components, and thus, cannot simply be considered a representation of oscillatory activity (Donoghue et al., 2020; Voytek et al., 2015).

Periodic brain activity represents rhythmic patterns of neural activity that occur at consistent intervals and are confined to a specific frequency range. In the power spectrum, oscillations are represented as narrowband peaks, which are indicative of higher levels of power relative to the surrounding background activity. Oscillatory activity can be characterized based on several parameters including: the center frequency, the power, and the bandwidth (Donoghue et al., 2020).

Aperiodic brain activity does not exhibit rhythmic patterns, instead, aperiodic activity represents a broadband spectral characteristic of EEG in which power decreases with increasing frequency in an approximately 1/f-like manner. Aperiodic activity is typically modeled in log-log space as a straight line with a negative slope (i.e., aperiodic exponent or slope) and an offset (vertical shift in overall power across the spectrum) (Donoghue et al., 2020). The aperiodic exponent reflects the rate at which power decreases with increasing frequency, whereas the offset reflects the total amount of broadband power across the spectrum. Contemporary studies suggest that this broadband component should not be viewed as un-interpretable "noise." Modeling of biophysical origins of EEG indicate that arrhythmic activity of neurons can be detected at the scalp level and can influence the shape of broadband spectral features through mechanisms related to synaptic kinetics and other characteristics of EEG generation (Brake et al., 2024). Therefore, aperiodic activity likely represents meaningful population-level dynamics, and not simply artifact from the measurement process.

An important consequence of the existence of both periodic and aperiodic brain activity is that the same band-limited measure can potentially represent different spectral causes. For example, the

apparent "alpha power" in the 8–12 Hz range could represent a true oscillatory peak, however, it could also be due to variations in the broadband background (offset) or changes in the steepness of the 1/f component (exponent). As such, it is becoming increasingly clear that EEG data should be treated as being composed of two distinct components: periodic and aperiodic (Donoghue et al., 2020).

2.3.4.2 Why traditional EEG analyses conflate components

Traditional EEG analysis approaches to quantifying oscillatory activity measure band-limited power in predetermined frequency ranges (e.g., the alpha band, 8–12 Hz). While this methodological approach has led to many influential studies, it makes an implicit assumption that band-limited power reflects changes in true oscillatory activity. However, since oscillatory peaks occur on top of a broadband aperiodic background, band-limited power estimates include both periodic and aperiodic contributions (Donoghue et al., 2020; Voytek et al., 2015).

The aperiodic component of the brain's electrical activity (its slope and/or offset) can have significant effects on the estimated power in any given band-limited range without altering the oscillatory activity. For example, a flattening of the aperiodic slope increases relative power at higher frequencies within a band, which may be interpreted as increased alpha or beta power when analyzed using standard methods. Shift in the aperiodic offset can cause an equal increase or decrease in power across all bands. That is than influencing band-limited estimates. Therefore, identical changes in alpha power can arise from different spectral mechanisms. For example like changes in oscillatory peaks, background activity, or both (Donoghue et al., 2020).

The conflation of oscillatory and aperiodic components presents a challenging problem when interpreting alpha power dynamics in cognition. The separation of oscillatory and aperiodic components is generally absent in the majority of reported alpha power studies. That leads to ambiguity regarding whether observed alpha power effects reflect rhythmic inhibition mechanisms or broader changes in cortical excitability. Empirical research has demonstrated that aperiodic activity varies with task requirements and cognitive states, suggesting that part or all of the variance in alpha power changes may be due to non-oscillatory mechanisms (Voytek et al., 2015).

Recent empirical work has demonstrated the direct impact of this issue. Utilizing time-resolved spectral parameterization, Bender et al. (2025) demonstrated that alpha power measures obtained through traditional methods combine oscillatory alpha activity with aperiodic activity during visual working memory tasks. After removing the aperiodic component, oscillatory alpha activity more accurately represented spatial information during memory maintenance, whereas aperiodic activity contained separate information about encoding.

In summary, the above considerations indicate that spectral parameterization methods, specifically those designed to separately estimate periodic oscillations from aperiodic background activity, allow for more accurate interpretation of neural signals underlying cognition (Donoghue et al., 2020; Bender et al., 2025).

2.3.4.3 Functional interpretations of aperiodic activity

In recent years, it has become increasingly clear that aperiodic activity is a meaningful contributor to the electrophysiology of cognitive functions and not simply 'noise' to be discounted when examining the functional organization of brain activity. Aperiodic activity is generally viewed as broadband, arrhythmic fluctuations in electrophysiological measures that vary systematically with cognitive function, task demand, and individual differences (Voytek et al., 2015; Donoghue et al., 2020), whereas oscillatory activity is thought to represent rhythmic coordination within frequency bands of interest. The aperiodic component of the EEG spectrum is often used to represent the overall conditions under which information processing occurs in large-scale neural population dynamics, rather than the coordinated activity of populations as represented by rhythmic oscillations.

One of the most common functional interpretations of the aperiodic spectral slope is that it represents the balance between excitatory and inhibitory synaptic processes within neural populations. Modeling studies, that are based on biophysical principles and computational models, are suggesting that the 1/f-like structure of electrophysiological signals is due to the temporal properties of synaptic currents, and that the exponent of the 1/f power-law relationship represents the relative contributions of excitation and inhibition (Voytek et al., 2015; Donoghue et al., 2020). Flatter slopes are then generally associated with relatively greater levels of excitation and/or less

inhibitory control. In comparison, steeper slopes represent inhibitory-dominant network states. It is important to note that the interpretation of the aperiodic slope as an indicator of the balance between excitation and inhibition does not mean that the slope directly indicates synaptic activity. It is rather suggesting, that the aperiodic slope is an indirect population-level measure of the balance between excitation and inhibition across large-scale neural networks.

Research has shown that aperiodic activity is behaviorally relevant (Herzog et al., 2024). As a result, neural gain can be seen as a functional consequence of E/I dynamics rather than an independent physiological signal. Gain refers to the sensitivity of neural populations to incoming sensory inputs. Because gain is determined by the relative levels of excitation and inhibition within a neural population, and because both excitation and inhibition modulate this sensitivity, variations in aperiodic activity provide a way to interpret changes in neural gain at the population level (Voytek et al., 2015; Pavlov & Kotchoubey, 2022). Aperiodic activity is believed to be a general indicator of global cortical state. The spatial and temporal characteristics of changes in the slope and offset of the aperiodic component of the EEG are generally wide-spread and smooth across time (Rawls & Sponheim, 2025), and are influenced by factors such as baseline excitability, arousal, and variability that are constant across task epochs. recent theoretical work has argued that aperiodic activity cannot be reduced to a single factor (Brake et al., 2024). Therefore, changes in aperiodic parameters should be considered as a composite signature of neural population dynamics, and not as a direct measure of a single physiological mechanism.

Collectively, the evidence supports the notion that aperiodic activity reflects large-scale network dynamics that are primarily determined by the balance of excitation and inhibition, with neural gain being a computational consequence of these dynamics, and global cortical state affecting the larger context in which oscillatory processes occur.

2.3.4.4 Relevance of aperiodic activity for cognition and attention

Evidence supports the idea that aperiodic activity is related to cognition and behavior, therefore aperiodic activity does not represent nonspecific background activity but instead represents meaningful neural activity. A number of resting-state and task-based EEG studies have shown that aperiodic activity varies with task engagement, cognitive effort and behavioral variability.

Numerous task-based studies have identified reliable distinctions in resting and active cognitive states using aperiodic activity. Rawls and Sponheim (2025), found that both the aperiodic exponent and offset changed with task performance and that these changes persisted even after baseline correction. Additionally, individual differences in the modulation of aperiodic parameters that occurred due to task performance correlated with behavioral performance and therefore suggest that aperiodic activity is relevant for cognitive functioning.

Pavlov and Kotchoubey (2022) argue that in order to understand cognition, background, scale free, neural dynamics must be considered. Pavlov and Kotchoubey propose that aperiodic activity is a representation of state dependent characteristics of neural systems including basal excitability, response to input, and susceptibility to variability.

Task based empirical evidence also demonstrates that aperiodic activity is influenced by cognitive effort and attentional demand. Liu et al. (2025), demonstrated that increases in the difficulty of a task and decreases in attentional suppression result in changes to the aperiodic exponent, regardless of the amount of oscillatory power present. This dissociation indicates that aperiodic dynamics are representative of effort related adjustments in neural processing at a global level, rather than the modulation of specific rhythmic mechanisms.

Additionally, aperiodic activity has been shown to be highly correlated to behavioral uncertainty and variability. Deodato and Melcher (2024) demonstrated that individual differences in the aperiodic exponent predicted variability in visual temporal perception, where flatter spectra were associated with greater perceptual noise and less consistent behavioral responses. Notably, the association between the aperiodic exponent and behavioral variability was independent of alpha oscillatory power. Similar associations between flatter aperiodic slopes, increased neural noise, and greater behavioral variability have been observed across a variety of cognitive domains (Voytek & Knight, 2015; Tran et al., 2020).

2.3.4.5 Why separating oscillatory and aperiodic activity matters for VWM

Separating the oscillatory and aperiodic components of the EEG signals is now a conceptual requirement to interpret the neural mechanisms of VWM. Traditional methods of analyzing the EEG signals focused on band-limited frequencies, assuming that changes in power reflected

oscillatory processes. A growing body of research indicates that the contributions of the broadband aperiodic activity are substantial to those power estimates and can result in systematic biases in interpretations when aperiodic activity is not controlled for (Brake et al., 2024).

In particular, the issue is very serious with respect to alpha-band studies of VWM. Changes in alpha power have long been considered as a measure of the neural mechanism of memory maintenance and attentional control. However, results from empirical investigations of alpha modulation in VWM have been inconsistent with respect to the direction and functional significance of the changes in alpha power. The study by Bender et al. (2025) provides conclusive evidence that the reason for these inconsistencies lies in the fact that alpha total power includes both the oscillatory alpha activity and the concurrent changes in aperiodic activity. By removing the aperiodic activity from the total alpha power, Bender et al. (2025) demonstrated that oscillatory alpha power encodes the spatial locations of memorized items during the delay period with greater reliability. Therefore, it is shown that alpha oscillations themselves carry spatially-specific information during the maintenance phase of VWM and not the broadband spectral changes.

Bender et al. (2025) identified a distinct functional role for aperiodic activity. Spatial information was decodable from the aperiodic activity during the encoding phase, but not during the maintenance phase. Thus, the aperiodic activity is most informative about encoding.

Liu et al. (2025) demonstrated that the aperiodic exponent is modified by both the load of targets and distractors during VWM tasks, but in an opposite manner, and independent of the oscillatory alpha power. These findings indicate that the aperiodic activity represents changes in the excitability of the global network and inhibitory control of the precision of the representation and its stabilization. This interpretation is consistent with the behavioral models of VWM that emphasize variability of representational precision rather than a fixed capacity for storing information (van den Berg et al., 2012).

Finally, Brake et al. (2024) demonstrated that aperiodic activity has a plausible neurophysiological basis. Therefore, ignoring aperiodic activity will lead to a systematic misinterpretation of broadband changes as changes in oscillatory mechanisms, especially in frequency bands like alpha where the peaks of oscillatory activity are usually small. Without this separation, changes in alpha

power may obscure different neural processes of VWM, including encoding, maintenance and variability in behavioral response. An open question that follows is whether the oscillatory and aperiodic components of the EEG signal have different roles at different stages of the task within VWM.

2.3.5 Dissociating Encoding and Maintenance in EEG

This chapter draws upon the theoretical and methodological framework outlined in previous chapters and explores whether separate neural systems operate during the encoding and maintenance phases of visual working memory (VWM). Recent advancements in EEG analysis have made possible the differentiation of contributions from oscillatory and aperiodic components to the neural signals that are collected at each stage of a VWM task. Therefore, researchers now question previous interpretations that regarded all neural markers collected during the course of a VWM task as contributing to a single continuous process.

Visual working memory (VWM) does not exist as a single process; rather, it exists as a collection of discrete processes. Most importantly, there are two primary stages of the VWM process: the initial encoding of the visual information, and the maintenance of that information during a delay. Research employing EEG has provided multiple neural markers that relate to VWM. However, the interpretation of those markers has generally regarded them as being indicative of a single, continuous process. A problem arises when neural activity is analyzed without regard for the task phase. Importantly, encoding and maintenance place different computational demands on the system, suggesting that they may rely on partially distinct neural mechanisms.

One example of this issue is alpha-band power. Alpha-band activity is commonly regarded as being indicative of working memory maintenance. Nonetheless, alpha-band power is typically estimated using band-limited methods. As a consequence, similar changes in alpha-band power may arise from different types of neural activity depending on when during the trial the activity occurs (Donoghue et al., 2020). More recently, it has been demonstrated that aperiodic activity varies systematically with cognitive states and levels of task engagement and can directly impact band-limited power estimates such as alpha-band power (Waschke et al., 2021). Thus, failure to separate the aperiodic component from oscillatory components makes it difficult to determine

whether observed alpha-band effects reflect maintenance-specific mechanisms or global shifts in neural state. Therefore, interpreting EEG markers of VWM requires analyses that are both phase-specific and component-specific. This ambiguity highlights the need for analyses that are both phase-specific and component-specific in order to accurately interpret EEG markers of VWM.

2.3.5.1 Time-resolved spectral parameterization as a methodological solution

A key methodological challenge in studying working memory with EEG lies in how spectral power is traditionally analyzed. EEG signals consist of both periodic oscillations and an aperiodic 1/f-like component that together define the power spectrum (Donoghue et al., 2020). Spectral parameterization models the EEG spectrum as comprising an aperiodic component and superimposed oscillatory peaks. This allows researchers to determine whether changes in band-limited power arise from oscillatory activity, aperiodic activity, or both.

In working memory research, both oscillatory and aperiodic activity change dynamically throughout a trial, and encoding and maintenance likely recruit different mechanisms over time. Time-resolved spectral parameterization is addressing this by estimating spectral parameters in sliding time windows. This is allowing both components to be tracked continuously across task phases (Bender et al., 2025). This approach enables the direct testing of whether specific spectral features are associated differently with encoding versus maintenance processes.

2.3.5.2 Evidence for temporally distinct mechanisms

Bender et al. (2025) demonstrated that oscillatory and aperiodic components contribute differently across task phases. Oscillatory alpha power was found to play important role in encoding spatial information during the delay period, which indicated a role in maintenance. In contrast, the aperiodic component was most informative during stimulus presentation, which is suggesting a role in encoding. These findings align with broader evidence that aperiodic activity reflects global neural state and attentional engagement (Waschke et al., 2021), but oscillatory alpha activity supports the retention of information over time. These results provide empirical support for a functional dissociation between encoding-related and maintenance-related neural dynamics. Importantly, these results indicate that alpha-band power cannot be interpreted as a unitary marker

of working memory. Instead, encoding and maintenance are supported by temporally and physiologically distinct neural mechanisms.

2.3.6 Implications of oscillatory and aperiodic EEG dynamics

Although the primary focus of this thesis is the oscillatory and aperiodic EEG dynamic contribution to visual working memory (VWM) in healthy subjects, this distinction could possibly have wider implications for developmental and clinical neuroscience. Research on neural oscillations and the aperiodic component of the EEG power spectrum has increasingly highlighted their importance and relevance for understanding large-scale brain dynamics in both typical development and neurodevelopmental disorders. Oscillatory activity in the alpha band showed to be involved in inhibitory processing, sensory gating and the allocation of attentional resources. Altered alpha activity has been seen in a number of clinical disorders such as attention-deficit hyperactivity disorder (Deiber et al., 2019). These alterations in alpha activity are frequently explained by differences in cortical excitability and inhibitory control, indicating that rhythmic activity represents the functional state of underlying neural circuits.

In addition, there has recently been a greater emphasis placed on separating oscillatory from aperiodic components of the power spectrum due to evidence that band-limited analyses of EEG power spectra can confound oscillatory activity with changes in the aperiodic part of the neural power spectrum, which is characterized by a $1/f$ -like distribution and represents non-oscillatory neural activity (Donoghue et al., 2020; Donoghue, 2025). Separating periodic and aperiodic components has therefore become an important analytical step for accurately characterizing neural spectral dynamics. This distinction is relevant because shifts in the aperiodic component can be influencing changes in oscillatory power across multiple frequency bands, which can potentially lead to misinterpretation if it is not explicitly accounted for (Donoghue, Dominguez, & Voytek, 2020; Donoghue, 2025). Developmental EEG research demonstrates that both oscillatory and aperiodic features change systematically across early life. That is reflecting the maturation of thalamocortical circuits and inhibitory interneuron networks that shape large-scale cortical dynamics (Wilkinson et al., 2024).

A large number of investigations now suggest that the aperiodic component is a function of the equilibrium state of excitatory and inhibitory signals in cortical circuitry. Studies and modeling data illustrate that an index of the aperiodic signal's spectral exponent could serve as a macroscopic representation of the equilibrium state of excitatory/inhibitory (E/I) balance in cortex (Gao et al., 2017; Donoghue, 2025), though the exact physiological representation of this relationship has yet to be resolved. Changes in E/I balance are often discussed in relation to neurodevelopmental and psychiatric disorders (autism, attention-deficit/hyperactivity disorder, schizophrenia). A similar idea has also been applied to aperiodic activity. Differences in aperiodic activity have been reported in several neurological and psychiatric conditions. However, there is substantial variability in the direction and magnitude of these changes across studies and populations (Donoghue, 2025). For example, increased values in the aperiodic exponent were found to be correlated with inhibitory dominance in large-scale neural networks and associated with both cognitive performance and genetic expression of GABAergic and glutamatergic signaling (Duma et al., 2024). At the same time, the heterogeneity of these findings highlights the importance of interpreting spectral measures cautiously and within their broader physiological and methodological context.

In this sense, the relevance of oscillatory and aperiodic EEG dynamics for neurodevelopmental disorders should be understood here as a broader implication rather than a direct focus of the present thesis. The primary goal of the current work is to examine the neural basis of working memory by studying how alpha oscillations and aperiodic activity contribute to encoding and maintenance in healthy individuals. This framework can serve as a starting point for future studies of how similar large-scale neural mechanisms may be differentially affected in atypical developmental or clinical populations.

2.4 Theoretical Summary and Research Hypotheses

This chapter summarizes the main theoretical insights presented in the preceding chapters. Information from these chapters is used to formulate the research question and hypotheses, that guide the empirical part of this thesis. In particular, it integrates behavioral models of visual working memory with recent advances in EEG research on oscillatory and aperiodic neural

dynamics. Based on this framework, the key research gaps is identified and the hypotheses tested in the empirical study are introduced.

2.4.1 Theoretical synthesis

The prior chapters provided reviews of the behavioral and neural mechanisms that have been suggested to account for the limits of visual working memory (VWM). A major debate at the behavioral level is about what type of model is better suited to describe the VWM capacity, i.e., whether the capacity should be thought of in terms of slot-based models which suggest a fixed amount of discrete storage units, or resource-based models which conceptualize capacity as a limited representational resource that is distributed across the number of items being remembered. Continuous report paradigms have contributed significantly to this debate since continuous reports allow for measurement of memory performance in terms of estimation error and precision (i.e., continuous measures), and not simply in terms of accuracy (i.e., discrete measures). Results from continuous-report paradigms have shown that recall variability typically increases as a function of set-size, suggesting that memory limitations reflect graded changes in representational fidelity rather than simply discrete storage failures. Mixture-modeling techniques have demonstrated that behavioral errors can result from a variety of sources (e.g., noise in the stored representation, swap errors, etc.) and, importantly, that behavioral data alone does not provide sufficient evidence to uniquely identify the neural mechanisms of VWM-capacity. Electroencephalography (EEG) offers a method for linking these behavioral phenomena to neural activity since it allows examination of the temporal characteristics of working memory processing. One of the most consistent EEG signatures that have been identified to date as being related to visual working memory are posterior alpha-band oscillations (8-12 Hz). The spatial location of items being stored in memory has been shown to be reflected by lateralized changes in alpha-power (the degree of power in alpha-band oscillations) and, further, that alpha-power during the delay-period of working memory tasks is typically modulated by memory-load and has been viewed as providing evidence for top-down control mechanisms that support stabilization of internal-representations and suppression of irrelevant sensory input during maintenance. This evidence suggests that oscillatory alpha-dynamics are critical for maintenance in visual working memory tasks.

However, EEG-signals also include a broadband aperiodic (1/f-like) component, which was previously considered to be background "noise" and is now viewed as a valid contributor to neural population activity. Research has established links between the slope and offset of the aperiodic-spectrum and various properties of cortical-dynamics (e.g., excitatory-inhibitory-balance, neural-gain, cortical-state). Importantly, both aperiodic and oscillatory activities occur in the same frequency range and, as a result, changes in band-limited measures of oscillatory-power (including alpha-power) will reflect some combination of aperiodic and oscillatory activity and do not directly measure changes in oscillatory synchronization per se. Recently developed methods (spectral-parameterization) enable separation of oscillatory-peaks from the aperiodic-background allowing researchers to derive more interpretable measures of neural activity.

Research conducted recently has indicated that the oscillatory and aperiodic components of the EEG signal may exhibit different patterns of modulation across the different stages of a working memory task. Specifically, studies employing time-resolved spectral-parameterization have found that the aperiodic-component exhibits strong modulation during the initial encoding phase (when the individual is first processing sensory information), whereas the oscillatory-alpha component is more reliable in its expression during the delay-phase (which includes both maintenance of internal-representations and spatial-prioritization of those representations).

These findings suggest that by temporally separating oscillatory and aperiodic activity, researchers will have a more accurate understanding of the mechanisms by which working memory operates. However, there is a paucity of research that examines the contributions of both types of spectral-components to the different phases of a working memory task within the context of a single paradigm. The present study therefore investigates oscillatory alpha activity and aperiodic EEG dynamics separately during the encoding and maintenance phases of a visual working memory task.

2.4.2 Research gap

Despite extensive research on alpha oscillations in visual working memory, there is an important methodological limitation in many of EEG studies. Specifically, many studies measure the activity in specific frequency bands (e.g., alpha) but do not separate the oscillatory activity from the

broadband aperiodic portion of the EEG signal. Since the oscillatory peaks and the aperiodic background overlap in the frequency domain, changes in band limited power (i.e., alpha power) can also represent shifts in the aperiodic background as opposed to actual changes in the degree of oscillatory synchronization. Therefore, it can be difficult to interpret the changes in alpha band modulations in visual working memory tasks when the contributions of oscillatory and aperiodic portions of the EEG signal are not separated.

The temporal organization of working memory tasks represents the second limitation. Typically, neural activity during visual working memory trials is analyzed either over the entire duration of the trial or over large time blocks (e.g., encoding + delay). However, working memory tasks involve two distinct cognitive phases: encoding of sensory information and the maintenance of this information during the delay. By analyzing neural activity in these phases separately, it may be better understood, how are the different neural mechanisms involved in forming a representation versus maintaining that representation.

Recent advances in methodology provide solutions to both of these limitations. Spectral parameterization methods allow researchers to decompose the EEG power spectrum into its oscillatory peaks and the aperiodic background component. Recent studies, that were using time resolved spectral parameterization, demonstrated that the contributions of the oscillatory and aperiodic components may vary across task phases. There, aperiodic dynamics is showing stronger modulation during encoding and oscillatory alpha activity is more closely associated with processes occurring during the maintenance period.

These findings are suggesting, that separating oscillatory and aperiodic activity and considering the temporal organization of working memory tasks, could lead to a more precise understanding of the neural mechanisms supporting visual working memory.

2.4.3 Research questions and hypotheses

The empirical part of this thesis builds upon the theoretical foundation presented in the preceding chapters. The goal is to explore the contribution of oscillatory and non-oscillatory components of EEG activity and how they contribute to different phases of the visual working memory task. Prior work has provided evidence that the process of visual working memory is composed of temporally

distinct processes including the early encoding of sensory information and the later maintenance of internal representations during the delay phase. Previous time-frequency analysis of EEG data has indicated that the activity of neural oscillations in the alpha band are associated with attentional control and the stabilization of memory representations. Recent methodological improvements have indicated that EEG signals include an aperiodic (non-oscillatory) component that represents large-scale dynamics of neural populations. This aperiodic component may modulate the estimated band-limited power in the oscillatory bands.

Since both the oscillatory and aperiodic components exist within the frequency domain, separating the two will likely provide a more detailed description of the neural processes involved in the visual working memory process. In particular, recent studies using spectral parameterization have suggested that aperiodic activity may be more strongly related to encoding processes, whereas oscillatory alpha activity may play a more prominent role during the maintenance of internal representations. Examining these components separately provides a way to better understand the temporal organization of neural mechanisms behind visual working memory.

In addition to the EEG hypotheses, behavioral performance was assessed using absolute recall error to verify that the set-size manipulation produced the expected memory-load effect.

Based on this theoretical framework, the thesis addresses the following research question:

How do oscillatory alpha activity and aperiodic EEG dynamics contribute to different phases of visual working memory, particularly encoding and maintenance?

To address this question, three hypotheses are tested.

H1 - Aperiodic encoding hypothesis

Aperiodic EEG activity will show stronger modulation during the encoding phase than during the maintenance phase.

Aperiodic activity has been proposed to reflect large-scale neural population dynamics related to cortical excitability and overall network state. Because encoding involves the initial processing and integration of sensory information, it is expected that changes in global cortical dynamics will

be most pronounced during stimulus presentation. Therefore, aperiodic activity is predicted to be more strongly modulated during encoding than during the delay period.

H2 - Alpha maintenance hypothesis

Posterior alpha oscillations will show stronger modulation during the maintenance period than during encoding.

Alpha-band oscillations have consistently been associated with attentional control and the stabilization of internal representations in visual working memory. In particular, posterior alpha activity has been linked to inhibitory mechanisms that help maintain relevant information while suppressing irrelevant sensory input during the delay period. For this reason, alpha oscillatory activity is expected to be more strongly modulated during the maintenance phase of the task.

H3 - Alpha estimation hypothesis

The encoding-maintenance alpha pattern will differ between traditional band-limited alpha power and decomposed oscillatory alpha peak amplitude.

Traditional band-limited alpha power may reflect both oscillatory alpha activity and broadband aperiodic contributions to the EEG spectrum. In contrast, spectral parameterization estimates oscillatory alpha peak amplitude after modelling the aperiodic background. Therefore, if the phase-related alpha effect observed with traditional band-limited power is partly influenced by broadband or aperiodic signal properties, this effect is expected to be reduced or not preserved when alpha is estimated as decomposed oscillatory peak amplitude. Because the two alpha estimates differ in operational definition, scale, preprocessing, and extraction procedure, this hypothesis was interpreted as a method-dependent alpha estimation hypothesis rather than as a direct test of which measure reflects the “true” alpha response.

Hypotheses formulated above guide the empirical investigation presented in the following chapter.

3. Methodology

3.1 Study overview

The present study investigated the neural mechanisms underlying visual working memory (VWM) by using electroencephalography (EEG). It was focusing on distinguishing oscillatory alpha activity from the aperiodic component of the neural signal. The study was designed to examine how these neural components contribute to different phases of working memory processing. And as well it studied, if separating these components provides a more precise characterization of neural dynamics.

Participants were performing a sequential color working memory task. Here, colored stimuli were presented one at a time. The number of items to be remembered varied across trials. There, set sizes were varying between 1, 3 and 5. That allowed the manipulation of memory load. After a retention interval, participants reported the color of a probed item using a continuous color wheel. That enabled measurement of memory precision on a continuous scale. The sequential nature of the task allowed a clear temporal separation between encoding and maintenance processes.

EEG data were recorded throughout the task using a 64-channel system. The experimental design enabled the definition of distinct temporal windows. These were corresponding to baseline, encoding and maintenance phases. These time windows were defined relative to the temporal structure of the stimulus sequence. They were also adjusted according to set size to ensure that comparable cognitive processes were captured across conditions.

The preprocessing and analysis of EEG data were structured to isolate induced neural activity and also to separate oscillatory from aperiodic components. Time-frequency representations were computed to quantify oscillatory dynamics, where the focus was on alpha-band activity (8-12 Hz). In the literature, alpha activity is associated with attentional control and the maintenance of internal representations. Besides that, spectral parameterization methods were used in the power spectrum to estimate the aperiodic component in the signal, which was indexed by the aperiodic exponent.

Based on these processed data, three hypothesis-driven analyses and one behavioral performance analysis were then conducted. The first analysis was examining if aperiodic activity is differentially modulated during encoding and maintenance. The second analysis examined baseline-relative posterior alpha activity during encoding and maintenance phases. The third analysis was directly comparing alpha estimates obtained using traditional band-limited approaches with those derived after separating the aperiodic component. That was done in order to understand how spectral decomposition influences the interpretation of alpha activity.

3.2 Participants

The primary recruitment process resulted in a total of 28 participants. Each participant participated in 2 experimental sessions. All participants ranged from 19-30 years in age, had either normal vision (and/or) correctable to normal vision, and indicated that they had never experienced any form of neurological or psychiatric disorder. All EEG data collected from each of the participants underwent a standardization of the same preprocessing steps and quality control procedures. Any participant whose data did not meet pre-defined rejection threshold levels were removed from analysis. Specifically, if greater than 30% of epochs were rejected, or greater than 20% of EEG channels were determined to be "noisy" by an automated detection system then the participant would have been removed from further consideration. Based upon these criteria, four participants' data were excluded. Also, one additional participant was removed since he/she only completed one session out of the two. The final sample totaled twenty-three and all subsequent analyses were conducted with this dataset.

3.3 Experimental Task

Participants performed a sequential visual working memory task based on a continuous color report paradigm called Color Wheel Task. This paradigm was selected because it is often used in the literature for investigating visual working memory. This task also has an ability to provide continuous measures of memory precision rather than binary accuracy (Bays et al., 2009; Zhang & Luck, 2008; van den Berg et al., 2012; Ma et al., 2014).

In each trial, a sequence of colored squares was presented one at a time at different spatial locations. The number of items was varying across trials (set sizes 1, 3 and 5). That allowed systematic manipulation of memory load. The sequential presentation format provided a temporal separation between encoding and maintenance processes and as well reduced overlap between item representations.

Each trial began with a fixation period consisting of a 2-second interval, which was followed by a random jitter between 100 and 500 ms. Subsequently, stimuli were presented sequentially: each item appeared for 200 ms and was then followed by a 300 ms inter-stimulus interval. After the final item was presented, the experiment introduced a retention interval of 1000 ms. At the end of the delay period, a response screen was displayed with continuous color wheel on it. Participants were instructed to report the color of a probed item by selecting the corresponding color on the wheel using a mouse. The response screen remained visible until a response was made.

To minimize perceptual confusions between items, a minimum angular distance of 44° was enforced between colors within each trial. The experiment consisted of 450 trials (150 per set size) per session.

The temporal structure of the task enabled the definition of distinct analysis windows corresponding to baseline, encoding and maintenance phases. Because encoding duration varied as a function of set size, time windows were defined relative to stimulus timing and adjusted across conditions to ensure comparability of neural measures.

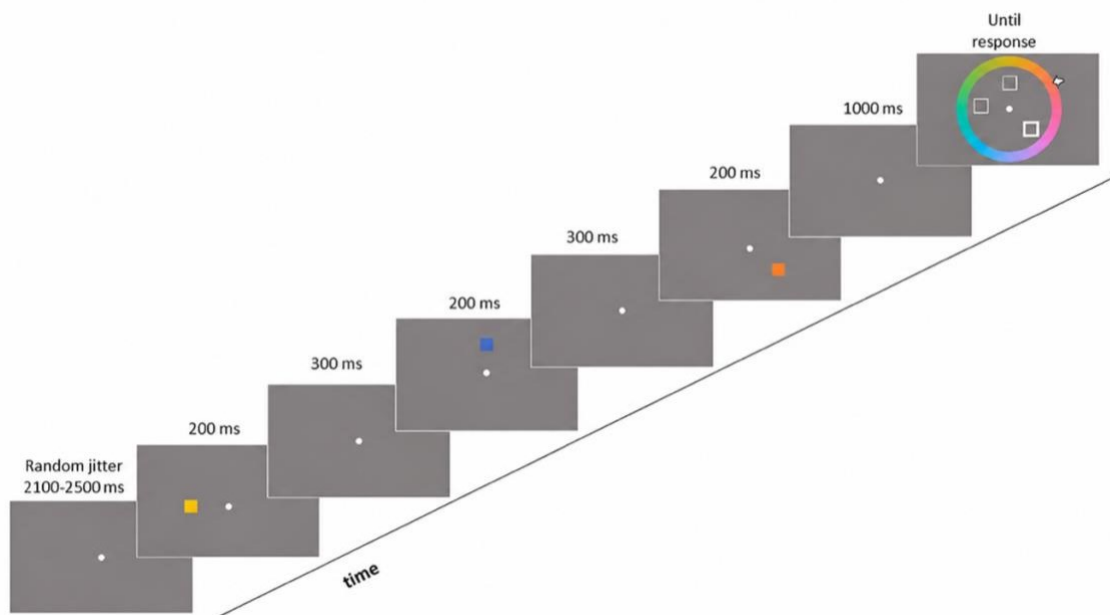


Figure 1. Sequential color visual working memory task.

Example trial structure of the sequential color continuous-report task. Participants encoded colored items presented sequentially, maintained them across a delay and then reported the color of the probed item using a continuous color wheel. Set sizes were 1, 3 and 5. Each participant completed 450 trials in each session. EEG was recorded from 64 channels.

3.4 EEG preprocessing and generation of derived data

3.4.1 EEG preprocessing pipeline

EEG data, that were used in this study were preprocessed in EEGLAB and FieldTrip in the MATLAB environment (Delorme & Makeig, 2004; Oostenveld et al., 2011). For this using a standardized pipeline was implemented. EEG data were sampled at 500 Hz. The preprocessing procedure was designed to remove noise and artifacts and to preserve neural signals of interest. Line noise at 50 Hz and 100 Hz was attenuated using ‘CleanLine’ plugin in EEGLAB. The continuous data were filtered firstly with high-pass at 0.1 Hz. Bad channels were identified using automated criteria, including prolonged flat signal and low correlation with neighbouring channels,

and were temporarily removed. Participants were excluded if more than 20% of channels were classified as bad.

For independent component analysis (ICA), a copy of the data was additionally high-pass filtered at 1 Hz, following recommendations that stronger high-pass filtering improves ICA-based artifact correction. ICA was performed using the infomax algorithm. The resulting ICA weights were then copied back to the main dataset. Components reflecting non-neural artifacts, including eye movements, blinks and muscle activity, were identified using automated classification and removed.

Following ICA correction, the data were low-pass filtered at 100 Hz. Previously removed bad channels were interpolated using spherical interpolation, and the data were re-referenced to the average of all EEG electrodes after removal of EOG channels. Datasets were then merged across sessions where applicable.

The continuous signal was divided into epochs corresponding to individual trials. Epoch length was adjusted according to set size. This made possible to capture the full temporal structure of every trial (baseline, encoding, maintenance). Epoch windows were -1500 to 2200 ms for set size 1, -1500 to 3200 ms for set size 3 and -1500 to 4200 ms for set size 5.

Artifact rejection was then performed at both the epoch and channel level. Trials were marked based on extreme voltage values, abnormal joint probability and kurtosis measures. Trial-by-trial procedures were used to interpolate noisy channels within individual epochs or reject epochs when artifact contamination exceeded predefined thresholds. Participants were excluded from next analysis steps if more than 30% of epochs were rejected or more than 20% of channels were classified as “bad”.

In this experiment the interest was on the induced oscillatory activity. Therefore, the aim was to isolate the induced non-phase-locked neural activity. It was done through computing the event-related potential (ERP) and subtracting it from each trial before time-frequency analysis. This helped to make sure that following analyses focused on ongoing oscillatory dynamics and not on evoked responses.

The cleaned and segmented data were then converted for use in FieldTrip and used in the following analyses.

3.4.2 Time-frequency decomposition

Time-frequency representations of the EEG signal were computed using the FieldTrip toolbox in MATLAB. The purpose of this step was to quantify oscillatory activity across both time and frequency, but at the same time preserving trial-level information.

Time-frequency decomposition was done using Morlet wavelets across a frequency range of 4 to 100 Hz in 1-Hz steps. The number of cycles was linearly increasing with frequency. It was ranging from 3 cycles at lower frequencies to 8 cycles at higher frequencies. This approach provided an appropriate trade-off between temporal and spectral resolution across the frequency spectrum. Time points of interest were defined from -0.8 s until the end of the epoch, with a temporal resolution of 20 ms. This window included the pre-stimulus baseline period and then also the encoding and maintenance phases of each trial. Power estimates were computed for each trial, channel, frequency and time point, resulting in time-frequency representations of the signal (channels $\times$ frequencies $\times$ time). Trial-level data were retained for subsequent analyses to enable statistical modeling at the single-subject level.

For visualization and power-based analyses, baseline correction was applied using a pre-stimulus interval from -0.8 to -0.5 s. Power values were expressed in decibel (dB) units relative to this baseline. These baseline-corrected time-frequency data were later used for the traditional posterior alpha analysis.

The resulting time-frequency data were used to extract oscillatory activity in specific frequency bands and regions of interest. These regions were especially posterior alpha-band activity (8-12 Hz). Also, these data provided input for upcoming spectral parameterization procedures.

3.4.3 Spectral parameterization

To separate oscillatory activity from the broadband aperiodic component of the EEG signal, spectral parameterization was performed using the FOOOF algorithm. FOOOF is modeling the

power spectrum like a combination of an aperiodic 1/f-like component and periodic oscillatory peaks above this background (Donoghue et al., 2020).

Power spectra were derived from the time-frequency data and averaged within predefined regions of interest. These ROIs included PFC, frontal, parietal and occipital regions, which were used for the descriptive visualization of aperiodic activity across regions. The main hypothesis-driven analyses focused on the occipital ROI, defined by PO7, PO3, POz, PO4, PO8, O1, Oz and O2. Spectra were estimated for baseline, encoding, retention, and final delay windows. The baseline window was defined from -0.8 to -0.5 s. Encoding windows corresponded to the stimulus-related periods. Maintenance was defined by averaging the relevant delay windows for each set size, so that the procedure was comparable to the averaging used for encoding.

Before model fitting, spectra were interpolated to obtain equally spaced frequency values. FOOOF was fitted using fixed aperiodic mode, with peak width limits of 2-8 Hz, a maximum of 6 peaks, a minimum peak height of 0.05, and a peak threshold of 1.5.

The main aperiodic parameter of interest was the exponent, which reflects the slope of the power spectrum in log-log space and provides an index of broadband neural activity. Periodic peak parameters were used to estimate decomposed alpha activity for the comparison with traditional alpha measures. This distinction was important because conventional band-limited alpha power may partly reflect changes in the aperiodic background rather than purely oscillatory activity.

The extracted FOOOF measures were used in the hypothesis-driven analyses: the aperiodic exponent was used for H1, while periodic alpha peak estimates were used for H3.

3.5 Hypothesis-specific data extraction

This section is describing how the behavioral and neural measures used in the statistical analyses were extracted. Behavioral recall error was extracted to assess task performance across set size and serial position. EEG analyses were based on the preprocessed datasets, that was described in the previous section, with separate MATLAB extraction procedures for each hypothesis. This section describes how subject-level estimates of the aperiodic exponent, posterior alpha activity, traditional alpha and decomposed alpha were generated from precomputed time-frequency and

FOOOF outputs. It also describes the relevant files, regions of interest, frequency bands, time windows, averaging procedures and exported data structures.

3.5.1 Behavioral absolute error extraction

Behavioral performance was assessed using absolute recall error in degrees. For each participant, trial-level behavioral data were extracted from the organized MATLAB files, including set size, serial position, and recall error. The same 23 participants included in the EEG analyses were retained for consistency across behavioral and neural analyses. Data from both sessions were combined, resulting in 900 trials per participant. Absolute error was computed as the absolute value of the signed recall error.

Trial-level data were then summarized by participant, set size and serial position. This produced one row per Subject $\times$ SetSize $\times$ SerialPosition. That resulted 207 rows in total and it was corresponding to 23 participants and nine available set-size/serial-position combinations. This summary was used for the behavioral statistical analysis and for plotting absolute error by set size and serial position.

A descriptive mixture-model visualization was also included to examine the structure of recall errors across set size and serial position. This visualization included four components: precision/concentration κ , target responses, non-target responses and uniform responses. Precision/concentration κ reflects how closely responses were clustered around the target color, with higher values indicating more precise recall. Target responses reflect the probability that the reported color was the probed one. Non-target responses reflect the probability that the reported color was an unprobed color. Uniform responses reflect responses that were not systematically centered on either the target or non-target color, hence representing guesses. This analysis was used only descriptively, and no inferential tests were applied to these components.

3.5.2 H1 - Aperiodic exponent extraction

Aperiodic activity was assessed using the exponent parameter obtained from spectral parameterization. The aperiodic exponent is reflecting the slope of the power spectrum in log-log space and it served as the neural metric of interest for H1.

For every participant, aperiodic exponent values were extracted from the precomputed FOOOF output files. Values were available for the predefined ROIs. The prefrontal ROI consisted of AF3, AFz, AF4, F7, F5, F3, F1, Fz, F2, F4, F6 and F8. Channels close to the eyes were excluded because they were often rejected or could still be partially contaminated by eye movements and blinks. The centro-frontal ROI consisted of FC5, FC3, FC1, FCz, FC2, FC4, FC6, C5, C3, C1, Cz, C2, C4 and C6. The centro-parietal ROI consisted of CP5, CP3, CP1, CPz, CP2, CP4, CP6, P7, P5, P3, P1, Pz, P2, P4, P6 and P8. The occipital ROI consisted of PO7, PO3, POz, PO4, PO8, O1, Oz and O2. The statistical analyses for H1 focused on the occipital ROI.

Time windows were selected as a function of set size. For set size 1, three windows were available, that were corresponding to baseline, encoding, and maintenance. The encoding window was 0.1-0.2 s and the maintenance window was 0.4-0.7 s. For set size 3, baseline was taken from window 1, encoding was averaged across stimulus-related windows 2, 4 and 6, which is corresponding to 0.1-0.2 s, 0.6-0.7 s and 1.1-1.2 s, and maintenance across delay windows 3, 5 and 7, corresponding to 0.3-0.5 s, 0.8-1.0 s and 1.4-1.7 s. For set size 5, baseline was taken from window 1, encoding was averaged across windows 2, 4, 6, 8 and 10, corresponding to 0.1-0.2 s, 0.6-0.7 s, 1.1-1.2 s, 1.6-1.7 s and 2.1-2.2 s, and maintenance across windows 3, 5, 7, 9 and 11, corresponding to 0.3-0.5 s, 0.8-1.0 s, 1.3-1.5 s, 1.8-2.0 s and 2.4-2.7 s.

Trial-level values were averaged within each participant and set size to get mean baseline, encoding and maintenance estimates. An Encoding - Maintenance difference score was computed and the number of non-missing trials, that is contributing to each estimate, was recorded. The resulting subject-level dataset had one row per participant and set size and had separate columns for baseline, encoding, maintenance and the difference score. It included 69 rows, corresponding to 23 participants across three set sizes. It was then exported from MATLAB for statistical analysis in R.

A second long-format dataset was generated for the serial-position analysis. Encoding and maintenance estimates were preserved separately for each serial position within each set size. That resulted in one row per participant, set size and serial position, and 207 rows in total. This allowed the encoding-maintenance comparison to be examined while accounting for serial position.

3.5.3 H2 - Posterior alpha extraction

Posterior alpha activity was extracted from precomputed induced time-frequency data. These data were already expressed in dB relative to the -0.8 to -0.5 s pre-stimulus baseline. No additional baseline correction was applied. The resulting values are representing baseline-relative induced alpha power in dB. There, more negative values are indicating stronger alpha suppression relative to baseline.

In line with H2, alpha activity was extracted from the posterior/occipital ROI defined by PO7, PO3, POz, PO4, PO8, O1, Oz and O2. Alpha activity was defined as power in the 8-12 Hz frequency range. For each participant and set size, values were averaged across the selected channels, alpha frequencies and time points within phase-specific encoding and maintenance windows. The final H2 dataset included the same 23 participants as the other EEG analyses.

Encoding windows were stimulus-related and varied by set size: 0.1-0.2 s for set size 1; 0.1-0.2 s, 0.6-0.7 s and 1.1-1.2 s for set size 3; and 0.1-0.2 s, 0.6-0.7 s, 1.1-1.2 s, 1.6-1.7 s and 2.1-2.2 s for set size 5. Maintenance was averaged across item-related delay windows rather than a single late delay interval: 0.4-0.7 s for set size 1; 0.3-0.5 s, 0.8-1.0 s and 1.4-1.7 s for set size 3; and 0.3-0.5 s, 0.8-1.0 s, 1.3-1.5 s, 1.8-2.0 s and 2.4-2.7 s for set size 5.

Mean dB-corrected alpha values were computed separately for encoding and maintenance. Maintenance - Encoding difference score was calculated for each participant and set size. The wide-format dataset had 69 rows and the long-format dataset used for the main R analysis had 138 rows. An additional serial-position dataset kept encoding and maintenance estimates separately for each serial position within each set size, resulting in 207 rows. This dataset was used to examine the phase comparison, but at the same time it accounted for serial position.

3.5.4 H3 - Traditional versus decomposed alpha estimates

To test H3, two operationalizations of alpha activity were compared. First one was the traditional band-limited alpha power derived from induced time-frequency data. The second one was the decomposed oscillatory alpha peak amplitude derived from spectral parameterization outputs. The aim was not to compare absolute alpha magnitudes, because the two estimates differ in scale,

preprocessing and operational definition. Instead, H3 was testing, if the encoding–maintenance phase pattern, that was observed in traditional alpha power was preserved when alpha was quantified as a decomposed oscillatory peak-amplitude estimate after separating oscillatory peaks from the aperiodic background.

Traditional alpha was extracted from the same baseline-corrected induced time-frequency data, posterior occipital ROI, 8-12 Hz frequency range and phase-specific windows used in H2. No additional baseline correction was applied and maintenance was averaged across all relevant item-related delay windows.

Decomposed alpha was extracted from the precomputed FOOOF outputs. For each trial, ROI and time window, oscillatory peaks between 8 and 12 Hz were identified. When more than one alpha-range peak was present, the strongest peak amplitude was retained. When no alpha-range peak was detected, alpha amplitude was coded as zero. Values were extracted from the occipital ROI, and baseline, encoding and maintenance windows were following the same set-size-specific logic as in the H1 aperiodic extraction.

The final H3 dataset was limited to the 23 participants with both traditional and decomposed alpha estimates. It was organized in long format, with one row per participant, set size, phase and method. That resulted in 414 rows in total. H3 was interpreted as a comparison of method-dependent alpha estimates. It was not interpreted as evidence that either method provides a uniquely correct measure of alpha activity.

3.6 Statistical analyses

Statistical analyses were conducted in R. Data exported from MATLAB were inspected for structure, missing values, and number of observations per participant. Variables were formatted as required for each analysis.

The main analyses used linear mixed-effects models with Subject as a random intercept. SetSize referred to memory load and had three levels: 1, 3, and 5. SerialPosition referred to the item's position in the sequential presentation stream and was centered when included. Phase referred to the task period from which the EEG measure was extracted: baseline,

encoding, or maintenance. In the main EEG models, Phase compared encoding and maintenance; baseline was used only in baseline-inclusive checks. Method, which was used only in H3, was referring to the alpha-estimation approach- traditional band-limited alpha power or decomposed oscillatory alpha peak amplitude.

Fixed effects included SetSize and SerialPosition for behavioral error, Phase and SetSize for H1 and H2, and Method, Phase and SetSize for H3. The dependent variables were mean absolute recall error for behavior, aperiodic exponent for H1, baseline-corrected posterior alpha power for H2 and alpha estimates for H3. Estimated marginal means were used for follow-up comparisons, with paired-sample t-tests or difference scores used as supplementary checks where appropriate.

Descriptive statistics and visualizations were computed for all analyses, and model diagnostics were inspected where relevant.

3.6.1 Behavioral error statistical analysis

Behavioral statistical analysis was performed in R. The dependent variable was mean absolute recall error in degrees, computed for each participant, set size and serial position. Subject was treated as a categorical variable, SetSize as a factor with three levels and SerialPosition as a centered numeric predictor.

A linear mixed-effects model was fitted with mean absolute error as the outcome variable, SetSize and SerialPosition as fixed effects and Subject as a random intercept:

$$\text{MeanAbsErrorDeg} \sim \text{SetSize} + \text{SerialPosition} + (1 \mid \text{Subject})$$

The interaction between SetSize and SerialPosition was not a part of the analysis, because serial position and set size are structurally related. It is because positions 4 and 5 occur only in the set-size 5 condition. The model therefore tested if absolute error was different across set sizes and if there was an overall serial-position trend after accounting for set size. Estimated marginal means were used to compare set sizes. Descriptive means and standard errors were calculated for each SetSize $\times$ SerialPosition combination and were used to visualize behavioral performance.

3.6.2 H1 - Statistical analysis

The subject-level dataset contained 69 observations, corresponding to 23 participants across three set sizes. Subject was coded as a categorical variable, and set size as a factor with three levels: 1, 3, and 5.

Because the updated extraction included baseline, encoding, and maintenance estimates, descriptive statistics were first calculated for all three phases. A baseline-inclusive linear mixed-effects model was also fitted as an additional check, with aperiodic exponent as the outcome variable, phase and set size as fixed factors, their interaction as a fixed effect, and subject as a random intercept. However, because H1 specifically concerned the comparison between encoding and maintenance, this model was not treated as the primary hypothesis test.

For the primary H1 analysis, the dataset was restricted to encoding and maintenance. The data were arranged in long format, with Phase containing two levels, Encoding and Maintenance, and Exponent used as the dependent variable. In this model, encoding and maintenance were treated as two levels of the categorical predictor Phase, rather than being subtracted from each other. The primary linear mixed-effects model included phase, set size, and their interaction as fixed effects, with subject as a random intercept:

$$\text{Exponent} \sim \text{Phase} \times \text{SetSize} + (1 \mid \text{Subject})$$

This model was testing whether the aperiodic exponent was different between encoding and maintenance. It also tested if exponent values were varying across set sizes and if the Phase effect depended on set size. Estimated marginal means were used to follow up the overall phase effect and to compare encoding and maintenance within each set size. Paired-sample tests comparing encoding and maintenance were also computed as supplementary descriptive checks. The linear mixed-effects model was treated as the primary inferential analysis.

Encoding - Maintenance difference scores were computed separately after extraction. These were used only for descriptive summaries and direction checks, not as the dependent variable in the primary mixed-effects model.

A second analysis was conducted to account for serial position. This analysis used the serial-position dataset, which preserved encoding and maintenance estimates separately for every serial

position within each set size. After reshaping into long format, the model included phase, set size, their interaction and centered serial position as fixed effects, with subject as a random intercept:

$$\text{Exponent} \sim \text{Phase} \times \text{SetSize} + \text{SerialPosition} + (1 \mid \text{Subject})$$

Serial position was included as a centered numeric predictor. The interaction between SerialPosition and SetSize was not part of the analysis because the two factors are partly structurally confounded. This model was testing if the Phase effect stayed after accounting for variation associated with serial position.

Estimated marginal means were extracted from both the primary and serial-position models. It was done to determine if H1 was supported and if the encoding-maintenance pattern was consistent across set size and robust to the inclusion of serial position.

3.6.3 H2 - Statistical analysis

The H2 analysis used posterior alpha values, that were extracted from the occipital/posterior ROI. The time-frequency data was baseline-corrected in dB relative to the prestimulus baseline. For this reason, the extracted alpha values were analysed directly, without applying another baseline correction. More negative values indicate stronger alpha suppression, that is relative to baseline.

Three datasets exported from MATLAB were used for this analysis. The first dataset was in wide format and contained Encoding, Maintenance and Maintenance - Encoding values. The second dataset was in long format and was used for the main mixed-effects model. The third dataset kept the serial-position information. It contained separate encoding and maintenance estimates for each serial position within each set size.

Before running the models, the datasets were checked for their structure, missing values, number of observations, and number of participants. Subject was coded as a categorical variable. Set size was treated as a factor with three levels: 1, 3 and 5.

The primary analysis used a linear mixed-effects model. Baseline-corrected posterior alpha power was used as the dependent variable. Phase, SetSize, and their interaction were included as fixed effects. Subject was included as a random intercept:

$$\text{Alpha} \sim \text{Phase} \times \text{SetSize} + (1 \mid \text{Subject})$$

This model tested whether posterior alpha suppression differed between encoding and maintenance. It also tested whether this phase difference changed with memory load. Estimated marginal means were then used for follow-up comparisons. These included the overall encoding-maintenance comparison, phase comparisons within each set size and set-size comparisons within each phase. Paired-sample t-tests between encoding and maintenance were also run as supplementary checks. However, the mixed-effects model was treated as the main inferential analysis.

A second mixed-effects model was used to take serial position into account. This analysis was based on the serial-position dataset. The data were reshaped into long format, with Phase containing two levels: Encoding and Maintenance. The model included Phase, SetSize, their interaction and centered SerialPosition as fixed effects. Subject was included as a random intercept.

$$\text{Alpha} \sim \text{Phase} \times \text{SetSize} + \text{SerialPosition} + (1 \mid \text{Subject})$$

The interaction between SerialPosition and SetSize was not included. This was because the two factors are in part confounded by the structure of the task. Later serial positions can only occur in the larger set sizes. This model therefore tested whether the encoding-maintenance alpha difference was still present after accounting for variation related to serial position.

For descriptive purposes, mean alpha values were calculated overall and separately by phase and set size. Subject-level Maintenance - Encoding difference scores were also calculated. These scores were used to check whether the direction of the effect was consistent across participants. Negative difference scores indicate stronger alpha suppression during maintenance.

3.6.4 H3 - Statistical analysis

H3 tested whether the encoding-maintenance pattern changed depending on how alpha activity was estimated. The analysis was based on a long-format dataset. This dataset included alpha estimates for every participant, set size, phase and estimation method. Two estimation methods

were compared: traditional band-limited alpha power and decomposed oscillatory alpha peak amplitude. Both were extracted from the occipital ROI. The final dataset had 414 rows. These corresponded to 23 participants, three set sizes, three phases, and two alpha estimation methods.

Descriptive statistics were first calculated for each Method $\times$ Phase combination. They were also calculated separately for each Method $\times$ Phase $\times$ SetSize combination. As a first check, a baseline-inclusive model was fitted to examine the full phase pattern across baseline, encoding and maintenance:

$$\text{Alpha} \sim \text{Method} \times \text{Phase} \times \text{SetSize} + (1 \mid \text{Subject})$$

This model used raw alpha values and included all three phases, so it was used only to describe the overall phase pattern. In contrast, the later Alpha_z model included only encoding and maintenance values and used alpha values standardized within each method. This allowed the encoding-maintenance effect to be compared between traditional and decomposed alpha without directly comparing their raw scales.

Traditional alpha power and decomposed alpha peak amplitude differ in scale. They also differ in how alpha activity is defined. Because of this, absolute differences between the two methods were not interpreted as differences in alpha magnitude.

For the main H3 analysis, only encoding and maintenance values were used. Separate mixed-effects models were first fitted for the two alpha estimates:

$$\text{Alpha} \sim \text{Phase} \times \text{SetSize} + (1 \mid \text{Subject})$$

These models tested the encoding-maintenance phase effect within each estimation method. This was done using each method's own measurement scale. For traditional alpha, more negative values indicated stronger alpha suppression, that is relative to baseline. For decomposed alpha, the values referred to oscillatory alpha peak amplitude from the spectral parameterization output.

The two alpha measures were on different scales. For this reason, the raw values weren't compared directly. Instead, alpha values were z-scored within each method. These standardized values were used in the main model comparing the two methods:

$$\text{Alpha_z} \sim \text{Method} \times \text{Phase} \times \text{SetSize} + (1 \mid \text{Subject})$$

The key effect for H3 was the Method $\times$ Phase interaction. This tested whether the encoding–maintenance difference was different for traditional and decomposed alpha estimates. Estimated marginal means were used for follow-up comparisons. These compared encoding and maintenance within each method, and also within each method and set size.

Phase-difference scores were also calculated as Maintenance - Encoding. Raw difference scores were used for descriptive interpretation. Standardized difference scores were used to compare the size of the phase effect across the two methods. Direction checks were also performed to see whether the Maintenance - Encoding difference was consistent across participants.

This analysis strategy made it possible to test if the traditional encoding-maintenance alpha pattern was also present in decomposed alpha estimates. At the same time, it avoided overinterpreting absolute differences between the two estimation methods.

4. Results

4.1 Behavioral performance

Behavioral performance was assessed by using mean absolute recall error, that was measured in degrees. The descriptive pattern showed a clear increase in error with set size. Error was lowest when only one item had to be remembered, $M = 10.83^\circ$. It increased at set size 3, $M = 25.75^\circ$ and was highest at set size 5, $M = 50.43^\circ$. The serial-position pattern was not identical across set sizes. For set size 3, the largest error appeared at the second serial position, while error was lower for the final item. For set size 5, errors were higher at the intermediate positions, especially positions 2 and 3. Error was again lower at the final position.

A linear mixed-effects model was later fitted with SetSize and centered SerialPosition as fixed effects and Subject as a random intercept. The model showed a significant main effect of SetSize, $F(2, 181) = 153.32$, $p < .001$. Follow-up comparisons confirmed that recall error was lower at set size 1 than at set size 3, $\beta = -19.2$, $SE = 3.10$, $t(181) = -6.20$, $p < .001$. It was also lower at set size 1 than at set size 5, $\beta = -48.1$, $SE = 3.22$, $t(181) = -14.91$, $p < .001$. In addition, error was lower at set size 3 than at set size 5, $\beta = -28.9$, $SE = 2.05$, $t(181) = -14.12$, $p < .001$.

SerialPosition also reached significance, $\beta = -4.25$, $SE = 0.75$, $t(181) = -5.65$, $p < .001$. This means that later serial positions were associated with lower absolute error after set size was taken into account. However, this result should be interpreted with caution, because serial position and set size are in part linked by the structure of the task.

Taken together, the behavioral results showed the expected memory-load effect. Participants made larger recall errors when more items had to be maintained. This confirms that the EEG analyses were based on task conditions in which memory load had a clear effect on behavior.

Effect / comparison	β	SE	Test statistic	p
SetSize	-	-	$F(2, 181) = 153.32$	$< .001$
Set size 1 - set size 3	-19.2	3.10	$t(181) = -6.20$	$< .001$

Set size 1 - set size 5	-48.1	3.22	$t(181) = -14.91$	< .001
Set size 3 - set size 5	-28.9	2.05	$t(181) = -14.12$	< .001
SerialPosition	-4.25	0.75	$t(181) = -5.65$	< .001

Note. The dependent variable was the mean absolute recall error in degrees. SerialPosition was centered and included as a numeric predictor.

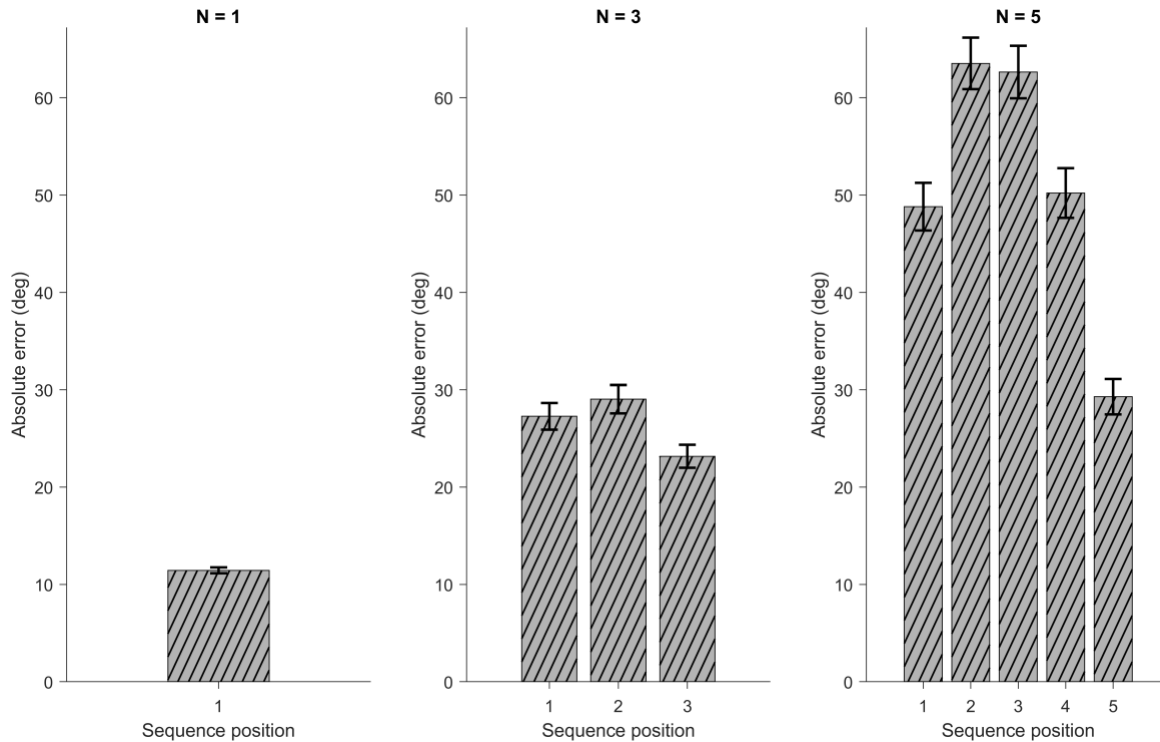


Figure 2. Absolute recall error by set size and serial position. Mean absolute recall error in degrees is shown separately for each set size and serial position. Error bars represent the standard error of the mean across participants. Behavioral data were averaged across both sessions for the 23 participants included in the EEG analyses. Absolute error increased with set size and showed a serial-position pattern, particularly in the set-size 5 condition, where intermediate positions showed the largest errors and the final position showed lower error.

4.1.1 Descriptive mixture-model visualization

In addition to the absolute-error analysis, the mixture-model visualization was inspected descriptively. This helped to show the structure of recall errors across set size and serial position

in more detail. The visualization included precision/concentration κ , target responses, non-target responses, and uniform responses. This analysis was used only descriptively and no inferential tests were applied to these components.

The general pattern was consistent with the absolute-error results. As shown in Figure 3A, precision/concentration κ was highest in the set-size 1 condition and was lower at higher set sizes. It was also evident that precision was higher for items presented at the end of the list. As shown in Figure 3B, a related pattern was visible for the probability of reporting the target items ($P(\text{target})$). $P(\text{target})$ decreased as the set size increased and in the set-size 5 condition, the decrease in target responses was most evident at serial positions 2 and 3. These were also the positions where absolute error was highest. As shown in Figure 3C, the probability of reporting non-target items ($P(\text{swap})$) increased as set size increased and it was higher mainly at serial positions 2 and 3. As shown in Figure 3D, the probability of guessing ($P(\text{uniform})$) stayed low in most conditions and did not show a strong increase.

This means that the larger errors at higher set sizes were probably not only caused by lower precision. In the set-size 5 condition, especially, participants also seemed to report fewer target colors and more non-target colors. Since this part of the analysis was only descriptive, it should not be read as a statistical result, but rather as additional support for the absolute-error findings.

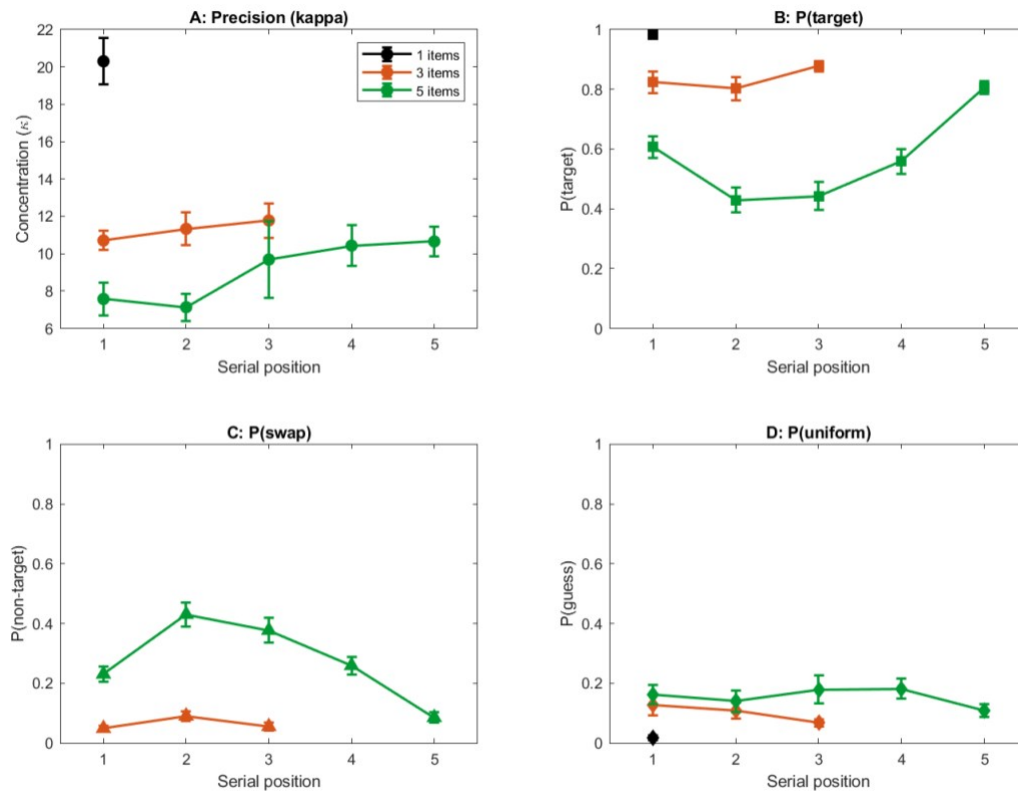


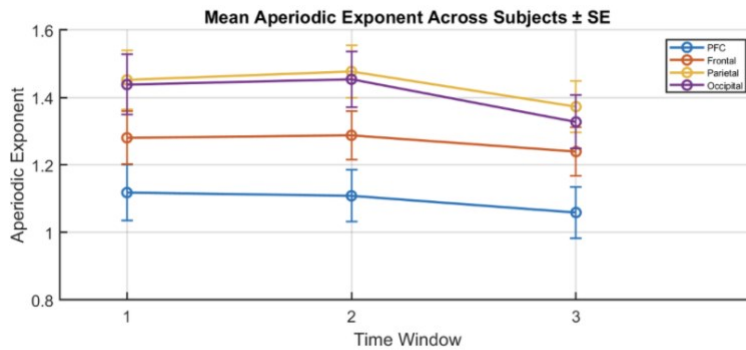
Figure 3. Descriptive mixture-model parameters by set size and serial position. Panel A shows precision/concentration κ , Panel B the probability of target responses, Panel C the probability of non-target responses and Panel D the probability of uniform responses. Parameters are shown separately for set sizes 1, 3 and 5 across serial positions. Error bars represent the standard error of the mean across participants. Descriptively, set size 5 showed lower precision, lower target-response probability and higher non-target-response probability, especially at intermediate serial positions, while uniform responses remained relatively low.

4.2 H1 - Aperiodic encoding hypothesis

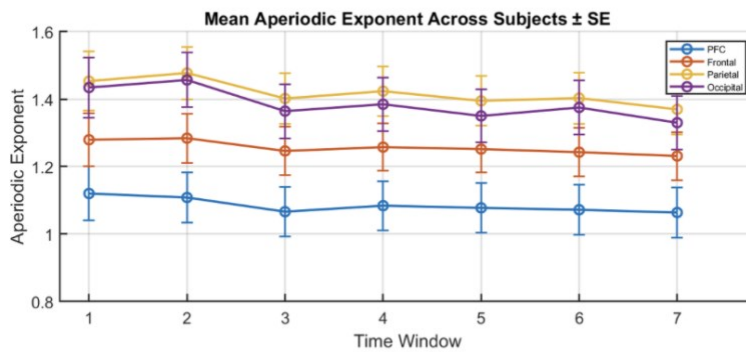
H1 was tested with a linear mixed-effects model. The dependent variable was the aperiodic exponent. Phase and SetSize were included as fixed effects, together with their interaction. Subject was included as a random intercept. The model used occipital ROI values from 23 participants across the three set sizes.

The descriptive values showed a higher aperiodic exponent during encoding, $M = 1.42$. During maintenance the mean value was lower, $M = 1.34$. This corresponded to an encoding-maintenance difference of 0.077. Baseline values were slightly higher overall, $M = 1.43$.

A. Set size 1



B. Set size 3



C. Set size 5

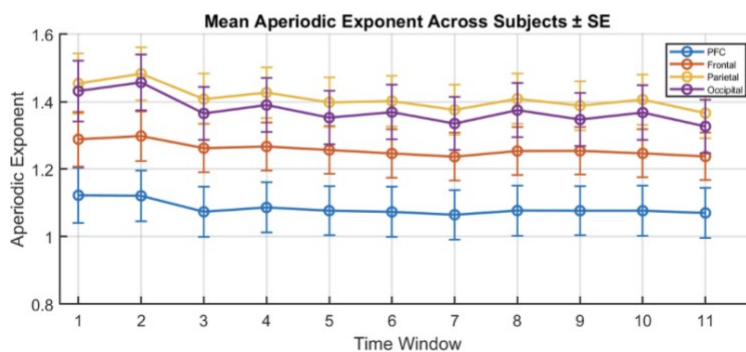


Figure 4. Descriptive aperiodic exponent across task windows and ROIs. Mean aperiodic exponent values are shown across task windows separately for set size 1 (Panel

A), set size 3 (Panel B) and set size 5 (Panel C). For set size 1, window 1 represents baseline, window 2 encoding and window 3 maintenance. For set sizes 3 and 5, window 1 represents baseline, even-numbered windows represent encoding periods and odd-numbered windows after baseline represent maintenance periods. Lines represent PFC, frontal, parietal and occipital ROIs. Error bars represent the standard error of the mean across participants. The figure is shown descriptively to illustrate the temporal pattern of aperiodic activity across ROIs. The statistical H1 analysis focused on the occipital ROI.

In the primary encoding-maintenance model, there was a significant main effect of Phase, $F(1, 110) = 458.74$, $p < .001$. SetSize was also related to exponent values, $F(2, 110) = 13.01$, $p < .001$. In addition, the effect of Phase was not the same across set sizes, as indicated by the Phase $\times$ SetSize interaction, $F(2, 110) = 48.84$, $p < .001$.

Follow-up estimated marginal mean contrasts showed that estimated marginal means were higher during encoding than during maintenance, $\beta = 0.077$, $SE = 0.004$, $t(110) = 21.42$, $p < .001$.

The encoding-maintenance difference appeared at each set size. It was largest at set size 1, $\beta = 0.127$, $SE = 0.006$, $t(110) = 20.37$, $p < .001$. At set size 3, the difference was smaller, $\beta = 0.057$, $SE = 0.006$, $t(110) = 9.24$, $p < .001$. At set size 5, the difference was also significant and remained similar in size to set size 3, $\beta = 0.047$, $SE = 0.006$, $t(110) = 7.48$, $p < .001$.

The baseline-inclusive model was used only as an additional check of the phase pattern. When baseline was included together with encoding and maintenance, Phase was significant, $F(2, 176) = 73.38$, $p < .001$. SetSize was not significant in this baseline-inclusive model, $F(2, 176) = 2.14$, $p = .121$. The Phase $\times$ SetSize interaction was also significant, $F(4, 176) = 4.77$, $p = .001$. Follow-up phase contrasts showed that the main difference was between maintenance and the other phases. Maintenance differed from baseline, $\beta = 0.094$, $SE = 0.008$, $t(176) = 11.39$, $p < .001$, and it also differed from encoding, $\beta = 0.077$, $SE = 0.008$, $t(176) = 9.27$, $p < .001$. Baseline and encoding were more similar. The baseline-encoding contrast was smaller and was not significant after Tukey correction for the three pairwise phase comparisons, $\beta = 0.018$, $SE = 0.008$, $t(176) = 2.12$, $p = .088$.

Serial position was then added in a separate model. In the serial-position model, the main effect of Phase remained significant, $F(1, 385) = 463.12, p < .001$. SetSize was also significant, $F(2, 385) = 3.49, p = .032$. Serial position was significant, $F(1, 385) = 171.44, p < .001$, and the Phase $\times$ SetSize interaction remained significant, $F(2, 385) = 35.78, p < .001$. Follow-up estimated marginal mean contrasts showed that the encoding-maintenance effect remained significant after this step, $\beta = 0.077, SE = 0.004, t(385) = 21.52, p < .001$. Serial position was significant as well, $\beta = -0.016, SE = 0.001, t(385) = -13.09, p < .001$. Later serial positions were associated with lower exponent values. This negative effect is indicating that each later serial position was associated with a small decrease in the aperiodic exponent, after it was accounted for phase and set size.

Overall, H1 was supported. Aperiodic exponent values were higher during encoding than maintenance across all set sizes, although the effect was largest at set size 1 and smaller at higher memory loads.

Effect / comparison	β	SE	Test statistic	p
Primary model: Phase	-	-	$F(1, 110) = 458.74$	$< .001$
Primary model: SetSize	-	-	$F(2, 110) = 13.01$	$< .001$
Primary model: Phase $\times$ SetSize	-	-	$F(2, 110) = 48.84$	$< .001$
Follow-up contrast: Encoding - Maintenance	0.077	0.004	$t(110) = 21.42$	$< .001$
Encoding - Maintenance, set size 1	0.127	0.006	$t(110) = 20.37$	$< .001$
Encoding - Maintenance, set size 3	0.057	0.006	$t(110) = 9.24$	$< .001$
Encoding - Maintenance, set size 5	0.047	0.006	$t(110) = 7.48$	$< .001$
Serial-position check: Encoding - Maintenance	0.077	0.004	$t(385) = 21.52$	$< .001$
Serial-position check: SerialPosition	-0.016	0.001	$t(385) = -13.09$	$< .001$

Note. Positive β values for Encoding - Maintenance indicate higher aperiodic exponent during encoding than maintenance. The baseline-inclusive model and serial-position model were additional checks.

4.3 H2 - Alpha maintenance hypothesis

To test H2, a linear mixed-effects model was used. The dependent variable was baseline-corrected posterior alpha power. Phase and SetSize were included as fixed effects, together with their interaction and Subject was included as a random intercept. The analysis used occipital ROI values from 23 participants across the three set sizes.

Descriptively, posterior alpha values were more negative during maintenance, $M = -5.05$ dB, than during encoding, $M = -3.96$ dB. This corresponded to a Maintenance - Encoding difference of -1.09 dB, indicating stronger baseline-relative alpha suppression during maintenance.

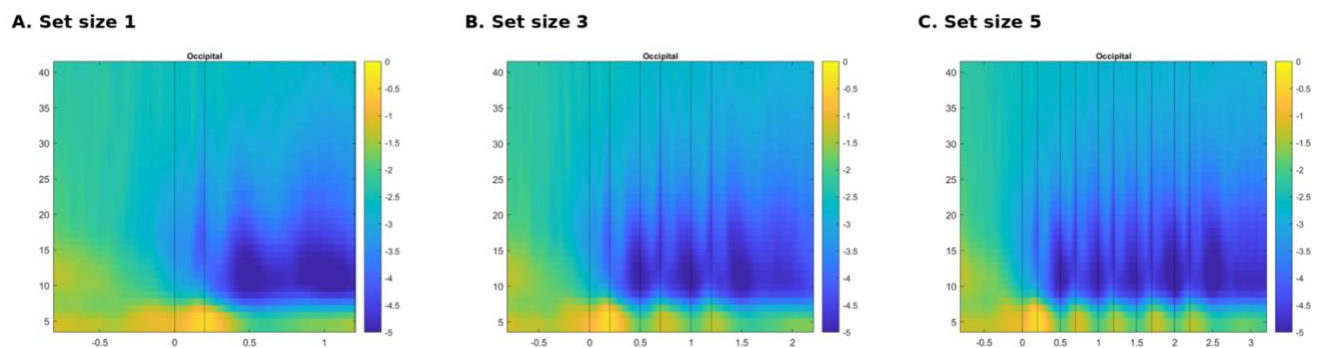


Figure 5. Occipital time-frequency power by set size.

Grand-average induced time-frequency power in the occipital ROI is shown for set size 1 (Panel A), set size 3 (Panel B) and set size 5 (Panel C). Values are expressed in dB relative to baseline; cooler colors indicate stronger baseline-relative suppression. Dotted vertical lines indicate task-relevant stimulus and delay windows. The closely spaced dotted lines mark each encoding period. There, the stimulus was presented for 200 ms and was followed by a 300 ms delay.

In the primary encoding-maintenance model, there was a significant main effect of Phase, $F(1, 110) = 142.59$, $p < .001$. The model also showed a significant main effect of SetSize, $F(2, 110) = 7.61$, $p < .001$, and a significant Phase $\times$ SetSize interaction, $F(2, 110) = 15.74$, $p < .001$.

Follow-up estimated marginal mean contrasts showed that encoding values were less negative than maintenance values, $\beta = 1.09$ dB, $SE = 0.092$, $t(110) = 11.94$, $p < .001$, which is indicating stronger alpha suppression during maintenance.

To understand the Phase $\times$ SetSize interaction, follow-up estimated marginal mean contrasts were used to compare encoding and maintenance within each set size. These contrasts showed that maintenance values were more negative than encoding values at all set sizes. The difference was largest at set size 1, $\beta = 1.81$ dB, $SE = 0.159$, $t(110) = 11.43$, $p < .001$. Smaller differences were found at set size 3, $\beta = 0.82$ dB, $SE = 0.159$, $t(110) = 5.16$, $p < .001$, and set size 5, $\beta = 0.65$ dB, $SE = 0.159$, $t(110) = 4.09$, $p < .001$. The interaction mainly reflected encoding values becoming more negative as set size increased, while maintenance values were comparatively similar.

Serial position was then included in a second model. In the serial-position model, the main effect of Phase remained significant, $F(1, 385) = 160.69$, $p < .001$. SetSize was not significant in this model, $F(2, 385) = 1.58$, $p = .206$. Serial position was significant, $F(1, 385) = 71.61$, $p < .001$, and the Phase $\times$ SetSize interaction remained significant, $F(2, 385) = 13.54$, $p < .001$. Follow-up estimated marginal mean contrasts showed that the encoding-maintenance difference remained significant after this step, $\beta = 1.08$ dB, $SE = 0.086$, $t(385) = 12.68$, $p < .001$. Serial position also had a significant effect, $\beta = -0.253$, $SE = 0.030$, $t(385) = -8.46$, $p < .001$. Alpha values became more negative at later serial positions.

At the subject level, all 23 participants showed a negative Maintenance - Encoding difference. The paired-sample t-test gave the same result, $t(22) = 8.54$, $p < .001$.

Overall, H2 was supported. Posterior alpha values were more negative during maintenance than during encoding. This means that alpha suppression relative to baseline was stronger during maintenance. The effect was present across all set sizes and was still significant when serial position was included in the model.

Effect / comparison	β	SE	Test statistic	p
Primary model: Phase	-	-	$F(1, 110) = 142.59$	$< .001$
Primary model: SetSize	-	-	$F(2, 110) = 7.61$	$< .001$
Primary model: Phase $\times$ SetSize	-	-	$F(2, 110) = 15.74$	$< .001$
Follow-up contrast: Encoding - Maintenance	1.09	0.092	$t(110) = 11.94$	$< .001$
Encoding - Maintenance, set size 1	1.81	0.159	$t(110) = 11.43$	$< .001$
Encoding - Maintenance, set size 3	0.82	0.159	$t(110) = 5.16$	$< .001$

Encoding - Maintenance, set size 5	0.65	0.159	$t(110) = 4.09$	$< .001$
Serial-position check: Encoding - Maintenance	1.08	0.086	$t(385) = 12.68$	$< .001$
Serial-position check: SerialPosition	-0.253	0.030	$t(385) = -8.46$	$< .001$

Note. Alpha values were baseline-corrected in dB. Positive β values for Encoding - Maintenance indicate that encoding values were less negative than maintenance values, reflecting stronger baseline-relative alpha suppression during maintenance. The serial-position model was an additional check.

4.4 H3 - Spectral decomposition hypothesis

For H3, the traditional alpha estimate was compared with the decomposed oscillatory alpha peak-amplitude estimate from the occipital ROI. These two values were treated as different ways of estimating alpha activity. Since they are not on the same scale, and are not defined in exactly the same way, the raw magnitudes were not compared directly. The main question was instead focused on whether both estimates showed the same encoding-maintenance pattern.

The descriptive pattern was clear for traditional alpha. Values were more negative during maintenance, $M = -5.05$ dB, than during encoding, $M = -3.96$ dB. That means that alpha suppression relative to baseline was stronger during maintenance. For decomposed alpha, the phase difference was much less visible. Mean peak amplitude was 0.421 during encoding and 0.406 during maintenance.

The two methods provided different descriptive patterns. In the method-specific traditional alpha model, there was a significant main effect of Phase, $F(1, 110) = 142.59$, $p < .001$. SetSize was also significant, $F(2, 110) = 7.61$, $p < .001$, and the Phase $\times$ SetSize interaction was significant, $F(2, 110) = 15.74$, $p < .001$. Follow-up estimated marginal mean contrasts showed that the Encoding - Maintenance contrast from the method-specific traditional alpha model was significant overall, $\beta = 1.09$, $SE = 0.092$, $t(110) = 11.94$, $p < .001$. The effect was present at each set size. It was largest at set size 1, $\beta = 1.81$, $SE = 0.159$, $t(110) = 11.43$, $p < .001$. It was smaller at set size 3, $\beta = 0.82$, $SE = 0.159$, $t(110) = 5.16$, $p < .001$, and at set size 5, $\beta = 0.65$, $SE = 0.159$, $t(110) = 4.09$, $p < .001$.

In the method-specific decomposed alpha model, there was also a significant main effect of Phase, $F(1, 110) = 4.80, p = .031$. SetSize was significant, $F(2, 110) = 7.99, p < .001$, but the Phase $\times$ SetSize interaction was not significant, $F(2, 110) = 0.39, p = .679$. Follow-up estimated marginal mean contrasts showed that the overall Encoding - Maintenance contrast from the method-specific decomposed alpha model was statistically significant, but the effect was very small, $\beta = 0.016, SE = 0.007, t(110) = 2.19, p = .031$. When the set sizes were examined separately, the contrast was not reliable. At set size 1, the result was close to the significance threshold, $\beta = 0.024, SE = 0.012, t(110) = 1.97, p = .052$. At set size 3, the contrast was smaller, $\beta = 0.013, SE = 0.012, t(110) = 1.04, p = .300$. At set size 5, it was also not significant, $\beta = 0.010, SE = 0.012, t(110) = 0.78, p = .435$.

For the comparison between methods, alpha values were standardized within each method. In this standardized method-comparison model, Method was not significant, $F(1, 242) = 0.00, p = 1.000$. Phase was significant, $F(1, 242) = 9.49, p = .002$, while SetSize was not significant, $F(2, 242) = 1.09, p = .337$. The Method $\times$ Phase interaction was significant, $F(1, 242) = 6.00, p = .015$. The Method $\times$ SetSize interaction was not significant, $F(2, 242) = 0.05, p = .948$, and the Phase $\times$ SetSize interaction was also not significant, $F(2, 242) = 1.02, p = .363$. The Method $\times$ Phase $\times$ SetSize interaction was not significant, $F(2, 242) = 0.69, p = .504$.

Follow-up contrasts from the standardized model were used to examine the significant Method $\times$ Phase interaction. For traditional alpha, the standardized phase difference was significant, $\beta = 0.556, SE = 0.142, t(242) = 3.91, p < .001$. For decomposed alpha, the same comparison was small and not significant, $\beta = 0.063, SE = 0.142, t(242) = 0.45, p = .656$.

As an additional check of the standardized model, Maintenance - Encoding difference scores were calculated from the z-scored alpha values. This difference-score analysis led to the same conclusion. The standardized Maintenance - Encoding difference was descriptively larger for traditional alpha, $M = -0.556$, than for decomposed alpha, $M = -0.063$. A paired comparison of subject-level average difference scores confirmed this difference, $t(22) = -10.74, p < .001$. The direction of the effect was also more consistent for traditional alpha. All 23 participants showed a negative Maintenance - Encoding difference for traditional alpha. For decomposed alpha, this was

less consistent, with negative differences in 15 participants and positive differences in 8 participants.

The results supported H3. Traditional alpha showed a maintenance-related suppression pattern. For decomposed alpha, the phase effect was much smaller and it wasn't reliable within the separate set sizes. This suggests that the encoding-maintenance alpha pattern depended on the estimation method. This should not be taken to mean that one method is the only correct measure of alpha activity. It shows that the interpretation of alpha modulation depends on the estimation method.

Effect / comparison	β	SE	Test statistic	<i>p</i>
Traditional model: Phase	-	-	$F(1, 110) = 142.59$	< .001
Traditional model: Phase $\times$ SetSize	-	-	$F(2, 110) = 15.74$	< .001
Traditional alpha: Encoding - Maintenance	1.09	0.092	$t(110) = 11.94$	< .001
Traditional alpha, set size 1	1.81	0.159	$t(110) = 11.43$	< .001
Traditional alpha, set size 3	0.82	0.159	$t(110) = 5.16$	< .001
Traditional alpha, set size 5	0.65	0.159	$t(110) = 4.09$	< .001
Decomposed model: Phase	-	-	$F(1, 110) = 4.80$	.031
Decomposed model: Phase $\times$ SetSize	-	-	$F(2, 110) = 0.39$	.679
Decomposed alpha: Encoding - Maintenance	0.016	0.007	$t(110) = 2.19$	.031
Decomposed alpha, set size 1	0.024	0.012	$t(110) = 1.97$	.052
Decomposed alpha, set size 3	0.013	0.012	$t(110) = 1.04$	.300
Decomposed alpha, set size 5	0.010	0.012	$t(110) = 0.78$	.435
Standardized model: Method $\times$ Phase	-	-	$F(1, 242) = 6.00$	.015
Standardized model: Method $\times$ Phase $\times$ SetSize	-	-	$F(2, 242) = 0.69$	.504
Standardized traditional alpha contrast	0.556	0.142	$t(242) = 3.91$	< .001
Standardized decomposed alpha contrast	0.063	0.142	$t(242) = 0.45$	.656
Difference-score comparison	-	-	$t(22) = -10.74$	< .001

Note. Traditional alpha values were baseline-corrected dB values, whereas decomposed alpha values represented oscillatory alpha peak amplitude. Raw values were not interpreted as absolute differences between methods. Standardized comparisons were based on values z-scored separately within method.

5. Discussion and Conclusion

5.1 Summary of main findings

This thesis examined visual working memory by distinguishing between aperiodic EEG activity, traditional band-limited posterior alpha power, and decomposed oscillatory alpha peak amplitude. The analyses tested how these measures differed between encoding and maintenance, and whether alpha-related conclusions depended on the method used to quantify alpha activity.

The behavioral results showed the expected effect of memory load. Absolute recall error was lowest when participants remembered one item and highest when they remembered five items. This pattern is in line with continuous-report studies showing that VWM performance becomes worse as the number of remembered items increases (Bays et al., 2009; van den Berg et al., 2012; Ma et al., 2014). Serial position was also significant. Later positions were associated with lower error after set size was taken into account, but this result should be interpreted cautiously, because later serial positions only occurred in the larger set-size conditions. The descriptive mixture-model visualization showed a similar pattern. At higher set sizes, especially when 5 items had to be remembered, the visualization suggested lower precision, fewer target responses and more non-target responses. Uniform responses stayed relatively low.

The first neural analysis supported H1. The EEG results showed that encoding and maintenance were not reflected in the same way across the different spectral measures. The aperiodic exponent was higher in encoding than in maintenance. This pattern was found across all set sizes and remained significant after serial position was included in the model. Later serial positions were also associated with lower exponent values. That is suggesting that aperiodic activity could be sensitive to the order in which items are encoded and to memory-load-related changes in representational precision. The size of the encoding-maintenance effect was not the same across memory loads. It was largest at set size 1 and smaller at set sizes 3 and 5. This suggests that encoding and maintenance differed in broadband spectral activity. However, the physiological meaning of the aperiodic exponent should still be interpreted carefully, because it is an indirect measure of neural activity (Voytek et al., 2015; Gao et al., 2017; Donoghue et al., 2020).

The second analysis supported H2. Baseline-corrected posterior alpha values were more negative during maintenance than encoding. That indicated stronger alpha suppression that is relative to baseline. This effect was present across all set sizes and remained significant after taking into account serial position. This finding should be interpreted as stronger maintenance-related alpha suppression, not as an increase in alpha power. This is consistent with previous work, that was linking alpha-band activity to working memory, attentional allocation, inhibition and regulation of task-relevant information (Jensen et al., 2002; Wianda & Ross, 2019; Pavlov & Kotchoubey, 2022).

The third analysis supported H3. Traditional band-limited alpha showed a robust encoding–maintenance difference, whereas decomposed oscillatory alpha peak amplitude showed only a very small overall phase effect that was weaker and not reliable within individual set sizes. The significant Method $\times$ Phase interaction showed that the alpha phase pattern depended on the estimation method. This does not mean that either method provides the only correct measure of alpha activity, but rather that alpha-related conclusions depend on how alpha is operationalized (Donoghue et al., 2020; Bender et al., 2025).

The findings show that encoding and maintenance are different in both aperiodic activity and alpha estimates. Encoding was associated with higher aperiodic exponent values and maintenance showed stronger posterior alpha suppression in traditional band-limited alpha. This alpha pattern was less clear after spectral decomposition. This is supporting the importance of distinguishing oscillatory and aperiodic EEG components when interpreting VWM dynamics (Bays et al., 2009; Christophel et al., 2017; Miller et al., 2018).

5.2 Interpretation in relation to previous literature

The findings of this thesis can be interpreted within the broader literature on visual working memory, particularly in relation to behavioral limits in continuous-report performance, phase-specific EEG dynamics, and the separation of oscillatory and aperiodic signal components.

5.2.1 Behavioral performance and task demands

The behavioral results confirmed that the sequential color continuous-report task produced a clear memory-load effect. Mean absolute recall error increased from 10.83° at set size 1, to 25.75° at set size 3 and to 50.43° at set size 5. This is consistent with the basic capacity limitation of VWM. Here, performance decreases as the number of remembered items increases (Luck & Vogel, 1997; Ma et al., 2014). Because the task used continuous report, this decline can be interpreted in terms of graded recall error and representational quality and not only as a binary failure to detect a change (Bays et al., 2009; van den Berg et al., 2012; Ma et al., 2014).

The descriptive mixture-model visualization suggested, that this behavioral cost reflected reduced precision and increased item confusions. Precision/concentration κ was highest at set size 1 and lower at set sizes 3 and 5. These findings are consistent with resource-based and variable-precision accounts. These are proposing that increasing set size reduces representational fidelity and that precision varies across items and trials (Bays et al., 2009; Fougner et al., 2012; van den Berg et al., 2012). Target-response probability also decreased with set size. Non-target responses increased especially at serial positions 2 and 3 in the set-size 5 condition. Large errors in continuous-report tasks can reflect reports of non-target items (Bays et al., 2009). This suggests that high-load performance reflected both noisier target representations and increased item confusions.

Random guessing doesn't appear to have been the primary factor either. The uniform component generally acts as an indicator of random guessing (Zhang & Luck, 2008). However, here this component remained relatively stable. Furthermore, it had a significantly smaller increase compared with the non-target response. The evidence for the overall increase in recall error appears to represent primarily lower precision, fewer reported target items and more reported non-target items; rather than just random guessing.

Serial position also contributed to the behavioral pattern. Later serial positions were associated with lower absolute error after accounting for set size. But this should be interpreted cautiously because later positions occurred only in larger set-size conditions. Descriptively, the set-size 5 condition showed the clearest pattern, with the highest absolute errors and non-target response probabilities at intermediate positions and lower error at the final position. This is compatible with

the sequential structure of the task, where middle items can be more vulnerable to interference and the final item could benefit from recency.

These findings show that increasing set size produced a structured change in VWM performance. These are characterized mainly by reduced target precision and increased item confusions rather than random guessing alone. This provides the behavioral context for interpreting the EEG results, where VWM-related changes were examined in relation to alpha-band oscillations and broadband aperiodic activity (Bender et al., 2025).

5.2.2 Aperiodic activity as an index of encoding-related neural state

There were significantly higher aperiodic exponents during encoding compared to maintenance phases. Thus, it seems that encoding was associated with a distinct broad-band spectral state compared to maintenance. This effect was seen within an area corresponding to the occipital region of interest and continued to be statistically reliable after controlling for serial position in the model. As the aperiodic exponent measures the slope of the power spectrum on a log-log scale, it implies that the broad-band spectral background differed between the formation of visual memory representations and their later maintenance.

Increasingly, researchers have come to understand that aperiodic activity can indicate general characteristics of neural population dynamics and cortical states rather than merely being "background" activity (Gao et al., 2017; Voytek et al., 2015; Donoghue et al., 2020). Therefore, the steeper slope during encoding may imply stronger modulation of neural population activity during the processing of visual information. However, caution should be exercised here due to the fact that the current data does not provide direct evidence regarding excitation-inhibition balance, synaptic activity, or other physiological mechanisms that may relate to the observed aperiodic effects.

It has been demonstrated recently that aperiodic activity may contain task-relevant information independent of oscillatory alpha activity (Bender et al., 2025). The findings reported above are consistent with this concept and extend it to the encoding-maintenance distinction, suggesting that aperiodic activity exhibited a greater degree of modulation when participants needed to encode visual information into working memory.

The Phase x SetSize Interaction demonstrated that the encoding-maintenance difference in aperiodic exponent was greatest at a set-size of 1 and decreased at set-sizes 3 and 5. Given that encoding-exponent values were greatest at a set-size of 1 and lower at higher set-sizes, while maintenance values did not show as clear of a trend, this cannot simply be viewed as a straightforward monotonic load effect. Instead, the differentiation between encoding-related and maintenance-related aperiodic activity appeared less pronounced when more items had to be processed.

This pattern fits with accounts emphasizing encoding as a demanding stage of VWM. Here, perceptual input needs to be transformed into internal representations for later maintenance (D'Esposito & Postle, 2015; Kim, 2019). It also relates indirectly to resource-based and variable-precision models. They are proposing, that increasing set size reduces representational quality because limited resources are distributed across more items (Bays et al., 2009; Bays, 2014; van den Berg et al., 2012; Ma et al., 2014). In the present thesis, behavioral error increased with set size and the encoding-maintenance aperiodic difference was smaller at higher set sizes. This is suggesting that increasing load affected both performance and encoding-related neural dynamics. This link remains indirect because trial-level brain-behavior relations were not tested.

5.2.3 Posterior alpha dynamics and the nature of maintenance processes

The second analysis showed a reliable difference in posterior alpha activity between encoding and maintenance. The values were more negative during maintenance. This point is important, because the time-frequency values were already baseline-corrected in dB. Therefore, the result should not be read as increased alpha power during the delay period. It indicates stronger alpha suppression, that is relative to the pre-stimulus baseline. The effect was present at all set sizes. It was also visible in all 23 participants and it remained significant after serial position was added to the model.

This result is not fully in line with the classical view of alpha activity during working memory maintenance. Here, increased alpha power during the delay period is often interpreted as functional inhibition or sensory gating, which may help with protecting stored information from interference (Jensen et al., 2002; Wianda & Ross, 2019). Wianda and Ross (2019), for example, reported alpha desynchronization during encoding and alpha synchronization during retention. However, this is

not the only pattern found in the literature. Alpha activity during the delay period can increase, but it can also decrease. This seems to be especially true in visual working memory tasks. Pavlov and Kotchoubey (2022) suggested, that alpha suppression during maintenance may reflect ongoing visual processing, rather than disengagement from visual areas.

The present result fits better with studies, that are linking lower posterior alpha during maintenance to continued involvement of task-relevant visual regions. One relevant example is Rodriguez-Larios et al. (2022). They described two posterior alpha rhythms with different functional roles during retention. One rhythm increased and the other one decreased and was associated with better accuracy. This decrease was interpreted as possible disinhibition of higher-order posterior areas, that are involved in maintaining visual information. From this perspective, the maintenance-related alpha suppression observed in the present thesis may reflect active retention of visual information. It should therefore not be understood simply as passive storage.

A similar interpretation is supported by broader models of working memory. These models describe working memory as a dynamic process and not only as continuous persistent activation. Distributed representations, recurrent interactions and transient bursts of activity could be also contributing to maintenance (Lundqvist et al., 2016; Lundqvist et al., 2018; Miller et al., 2018). These accounts do not directly predict posterior alpha suppression. Still, they make the present finding easier to interpret, because they suggest that delay-period activity can be active, temporally structured and not necessarily stable over the whole maintenance period.

The Phase $\times$ SetSize interaction is adding another point. Load effects were expressed more clearly during encoding than during maintenance. The encoding-maintenance difference was largest at set size 1, and smaller at set sizes 3 and 5. This was mainly because encoding values became more negative as load increased. Maintenance values were in contrast already strongly suppressed across set sizes. In this sense, the pattern is consistent with the idea that encoding is an important bottleneck in VWM capacity. The increase in the number of items already affected posterior alpha activity during the formation of memory representations (Vogel et al., 2005; Bays et al., 2009).

This interpretation also needs to be considered in relation to H3. The strong encoding-maintenance effect found in traditional band-limited alpha was not preserved to the same extent when alpha was

estimated as decomposed oscillatory peak amplitude. For this reason, the H2 effect should not be treated as a pure change in oscillatory alpha alone. It is better described as a traditional band-limited alpha effect, which may also include broader spectral or aperiodic contributions.

5.2.4 Method-dependent alpha effects and spectral parameterization

The encoding-maintenance alpha pattern depended on how was alpha activity estimated. Traditional band-limited alpha showed stronger baseline-relative suppression during maintenance than during encoding. However, when alpha was estimated as decomposed oscillatory peak amplitude, the phase difference was much smaller and was not reliable within the individual set sizes. This means that H3 should not be understood as showing a complete absence of phase modulation in decomposed alpha. The important point is that the strong phase pattern found with traditional alpha was not preserved to the same extent after doing spectral parameterization.

This matters for how the alpha-band effect is interpreted. The traditional band-limited measure is not a pure estimate of oscillatory alpha activity. It reflects all signal power within the selected 8-12 Hz range. That means that both oscillatory peaks and the broadband aperiodic background can contribute to it (Donoghue et al., 2020). This is important, because aperiodic activity can also change with cognitive state and task demands. For this reason, a change in alpha-band power should not automatically be interpreted as a change in oscillatory alpha alone (Voytek et al., 2015; Gao et al., 2017; Donoghue, Dominguez, & Voytek, 2020). The standardized Method $\times$ Phase comparison supported this interpretation. The difference between traditional and decomposed alpha was not only a raw scale difference. It also reflected that the phase pattern itself was different between the two estimates.

At the same time, this result should not be overinterpreted. It does not prove that the traditional alpha effect was caused by the aperiodic component. Traditional and decomposed alpha differed not only in whether spectral parameterization was applied, but also in their operational definition and extraction procedure. The traditional estimate reflected average 8-12 Hz baseline-corrected power, whereas the decomposed estimate reflected FOOOF-derived peak amplitude. For this reason, the result is best interpreted as evidence that alpha effects are method-dependent. It is not evidence that one estimate is correct and the other one is incorrect.

This interpretation also fits with Bender et al. (2025), who showed that oscillatory and aperiodic components can contribute differently to working memory-related EEG signals. In the present thesis, this is why the comparison between traditional and decomposed alpha is useful. It helps to show if the band-limited alpha effect is more likely to reflect oscillatory alpha activity, broader aperiodic activity or some combination of both.

5.2.5 Implications for models of visual working memory

The present findings do not directly distinguish between slot-based, resource-based and variable-precision models of visual working memory. However, they seem to fit better with a graded and multi-component view of VWM performance than with a simple stored/not-stored distinction. Slot-based models are emphasizing storage probability and capacity limits (Luck & Vogel, 1997; Zhang & Luck, 2008), whereas resource-based and variable-precision accounts are more focused on graded changes in precision, noise and representational fidelity across items and trials (Bays et al., 2009; Bays, 2014; van den Berg et al., 2012; Ma et al., 2014).

Behaviorally, recall error increased from set size 1 to 3 and from set size 3 to 5. The descriptive mixture-model visualization suggested, that this cost was related to lower precision, lower target-report probability and increased non-target responses, especially at set size 5. This pattern is supporting the idea that higher load affected representational quality. At the same time, it also suggests that item confusions contributed to performance. Therefore, the behavioral results fit better with a graded and multi-component account of VWM limitations than with a purely binary failure of storage.

The EEG results are adding another level to this interpretation. These behavioral limits were accompanied by phase-specific neural differences. The higher aperiodic exponent during encoding is relevant to models emphasizing encoding precision, neural variability and representational quality (Bays, 2014; van den Berg et al., 2012; Ma et al., 2014), although this link remains indirect because trial-level brain-behavior relations were not tested. The stronger posterior alpha suppression during maintenance is consistent with dynamic accounts, where retained information depends on distributed activity across sensory and association regions, rather than on a fixed storage buffer alone (D'Esposito & Postle, 2015; Christophel et al., 2017; Miller et al., 2018).

At the same time, H3 is showing that neural markers must be interpreted carefully. The traditional alpha effect was much weaker when alpha was estimated as decomposed oscillatory peak amplitude. This is suggesting that band-limited alpha may partly reflect broader spectral contributions, including aperiodic or broadband activity (Donoghue et al., 2020; Bender et al., 2025). Because of this, links between EEG markers and concepts such as inhibition, storage, precision or active maintenance depend also on how the signal is quantified.

Overall, the findings support a dynamic and graded view of VWM, where performance depends on representational quality, target selection and item confusions, while neural activity differs across encoding and maintenance. The results do not give direct evidence for one specific model. Rather, they show that combining behavioral measures with separated oscillatory and aperiodic EEG components can provide a more precise framework for relating VWM performance to neural dynamics.

5.3 Limitations

Few limitations should be considered when interpreting the present findings. First, the analyses were based on predefined encoding and maintenance windows, and on measures averaged across trials, time points and posterior/occipital ROIs. This provided stable estimates for statistical modelling, but may have reduced finer temporal, spatial or trial-level variability. This is relevant especially because working memory is often described as a dynamic and temporally structured process, not only as a stable storage state (Lundqvist et al., 2016; Lundqvist et al., 2018; Miller et al., 2018). Second, the behavioral interpretation is limited by the level of analysis. Mean absolute recall error showed a clear set-size effect. However, this measure by itself does not separate reduced precision, guessing, non-target responses or other sources of error. The descriptive mixture-model visualization helped to illustrate these components, but was not used as the primary inferential analysis. Third, serial-position effects should also be interpreted carefully. Serial position was included as an additional predictor in the behavioral, H1 and H2 analyses. However, it was partly confounded with set size, because later positions appeared only in the larger set-size conditions. For this reason, these effects should be understood as overall trends after accounting for set size, not as fully independent serial-position mechanisms. Finally, both aperiodic and alpha-related interpretations remain methodologically constrained. The aperiodic exponent characterizes

broadband spectral structure, but its physiological meaning in working memory remains indirect, especially when it is discussed in relation to excitation–inhibition balance (Donoghue et al., 2020). Similarly, H3 should be understood as a method-dependent alpha estimation analysis, not as a test of which measure reflects the “true” alpha response. Traditional and decomposed alpha differed in operational definition, scale and extraction procedure. Therefore, the weaker phase effect in decomposed alpha cannot prove that the traditional alpha effect was caused by the aperiodic component. This thesis focused on alpha-band activity and the aperiodic exponent. Other frequency bands, connectivity patterns and more spatially resolved neural dynamics were not examined. Since working memory is supported by distributed and multi-frequency neural processes (Christophel et al., 2017; Miller et al., 2018), the present findings provide only a partial characterization of the neural mechanisms underlying visual working memory.

5.4 Future directions

The present findings suggest several directions for future research. First, future analyses could be more time-resolved and more focused on trial-level variability. In the present thesis, the analyses were based on predefined encoding and maintenance windows. This was useful for testing the main hypotheses, but it also means that more fine-grained temporal dynamics were not examined. Future work could therefore combine spectral parameters with analyses of transient neural events, such as burst-like activity. This could help to show, how broader brain states interact with moment-to-moment working memory dynamics (Lundqvist et al., 2016; Lundqvist et al., 2018; Miller et al., 2018). Second, EEG measures should be related more directly to behavior. It could test whether the aperiodic exponent, traditional alpha suppression or decomposed alpha peak amplitude predict precision, target responses, non-target responses or guessing. Future studies should also try to separate serial position from memory load more clearly. In the present task, later serial positions were present only when set size was larger. Because of this, the serial-position effects cannot be treated as fully independent from load. If the design allowed serial position and set size to be less confounded, it would be easier to say whether these effects are reflecting recency, interference, or load-dependent changes during encoding. Traditional and decomposed alpha should also be compared with methods that are more similar to each other. For example, both traditional and aperiodic-adjusted alpha estimates could be extracted from the same spectra. The ROIs, time

windows and alpha metrics could also be matched. This would make the comparison more direct, especially when testing whether traditional alpha effects are reduced after accounting for the aperiodic background (Donoghue et al., 2020; Bender et al., 2025). The same approach could be also extended beyond alpha-band activity and the aperiodic exponent. Other frequency bands, spatially resolved dynamics and connectivity between regions were not examined here. However, they may provide a broader picture of distributed and multi-frequency working memory mechanisms (Christophel et al., 2017; D’Esposito & Postle, 2015; Lundqvist et al., 2011; Lundqvist et al., 2016). Combining EEG with behavioral modelling, neurophysiological measures or clinical comparisons could also help to clarify the relevance of aperiodic activity as a marker of working memory function (Gao et al., 2017; Donoghue et al., 2020).

5.5 Conclusion

The present study investigated neural dynamics of visual working memory by looking at behavioral performance, traditional posterior alpha activity, decomposed oscillatory alpha peak amplitude and the aperiodic component of the EEG signal. Behaviorally, absolute recall error increased with set size. This confirmed that the task produced a clear memory-load effect.

Aperiodic activity showed stronger modulation during encoding than during maintenance. This is suggesting that memory formation was associated with phase-specific broadband neural activity. Traditional posterior alpha activity also differed between encoding and maintenance. Here, there was stronger baseline-relative alpha suppression during the maintenance period. However, this phase-related alpha pattern was much weaker when alpha was estimated as decomposed oscillatory peak amplitude. Because of this, conclusions about alpha dynamics are depending on how alpha activity is operationalized.

The findings are showing that it is important to distinguish periodic and aperiodic EEG components when interpreting spectral dynamics in visual working memory. In this thesis, combining behavioral analysis, traditional time-frequency analysis and spectral parameterization helped to interpret EEG effects more carefully in relation to visual working memory processes.

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