Electrophysiological underpinnings of individual differences in verbal working memory

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Abstract

Given the importance of working memory (WM) for everyday cognitive functioning, understanding the architecture of WM is crucial for understanding human behavior. Only a limited progress has been made to explore neural underpinnings of individual capacity limits despite 25 years of extensive psychophysiological WM research. Particularly, most psychophysiological studies target only the short-term memory (STM) construct, while STM is only a part of the working memory responsible for the storage of sensory information. Much less effort has been devoted to study brain mechanisms supporting the executive component of WM – the part that allows the manipulation of information. Therefore, I pursued two main goals in the current work: (1) to study electrophysiological correlates of sensory storage and central executive components of WM and (2) to assess the contribution they make to individual differences in WM performance.

To reach these goals, a large number of participants (N = 156) were tested in WM tasks of average to high complexity with and without manipulations, while EEG was recorded. Increasing the complexity of the tasks allowed to increase the variance in order to avoid ceiling effect in performance and to better distinguish low and high performers. Introduction of the task with mental manipulations allowed to assess the contribution of executive WM components separately from its storage components.

As expected, WM performance decreased with increasing memory load and was worse in the more difficult manipulation task than in the easier retention task. In accordance with an a priori hypothesis, manipulations in WM enhanced theta activity; hence, confirming the role of middle frontal theta in the executive functions and its relationship with the central executive component of WM. On the other hand, the hypothesis concerning the role of alpha in filtering out distractors was not confirmed. Moreover, alpha activity was not related to individual WM performance. Instead, lower beta activity in the frequency range of 16-22 Hz emerged as a potential candidate to affect the individual WM capacity; the mechanism of this effect remains unknown. Supposedly, beta oscillations can influence WM performance through regulation of the ability to execute mental manipulations. Finally, the results of the present study confirm the hypothesis that executive components of WM, rather than its components related to sensory storage, play the decisive role in individual WM capacity limits.

Zusammenfassung

Arbeitsgedächtnis (kurz: AG) ist eine Funktion, deren Bedeutung für unser tägliches kognitives Funktionieren nicht überschätz werden kann. Angesichts dessen ist das Verständnis der kognitiven Struktur des AG und seiner neurophysiologischen Grundlagen sehr wichtig für das Verständnis des menschlichen Verhaltens im Allgemeinen. Dennoch gibt es keinen großen Fortschritt in der Erforschung der Möglichkeiten und Grenzen des menschlichen AG und insbesondere dessen neurophysiologischen Basis trotz 25 Jahre intensiver Experimente in diesem Bereich. Die meisten bisherigen Studien sprechen lediglich das Konstrukt des Kurzzeitgedächtnisses (KZG) an, obwohl das KZG nur ein für Speicherung und Behalten der Information zuständiger Teil des AG ist. Viel weniger wird die andere Komponente des AG untersucht, nämlich die exekutive Komponente, die uns erlaubt, Informationen im Gedächtnis zu manipulieren. Dementsprechend hatte die vorliegende Arbeit zwei Ziele: (1) elektrophysiologische Korrelate der zwei Komponenten des AG (sensorische Speicherung und Behalten einerseits, exekutive Kontrolle andererseits) zu untersuchen und (2) den Beitrag dieser Komponenten zu den individuellen Unterschieden in der AG-Leistung einzuschätzen.

Um diese Ziele zu erreichen, habe ich eine große Stichprobe von 156 Probanden mit Hilfe von AG-Aufgaben verschiedener Komplexitätsgrade, mit und ohne mentale Manipulation, untersucht. Während dessen wurde das EEG registriert und später im Zeitbereich (ereigniskorrelierte Potentiale) und Zeitfrequenzbereich (EEG-Oszillationen) analysiert. Hohe Aufgabenkomplexität führte zur Zunahme der Streuung und zur besseren Differenzierung zwischen Teilnehmern mit hoher und niedriger AG-Leistung. Einführung der Manipulationsaufgabe erlaubte den Beitrag der exekutiven Komponenten getrennt von den Komponenten der Speicherung und des Behaltens zu untersuchen.

Wie erwartet nahm die behaviorale Leistung mit zunehmender Gedächtnisbelastung ab; sie war auch niedriger in der schwierigeren Manipulationsaufgabe als in der leichteren Behaltensaufgabe. Die Hypothese wurde bestätigt, dass Manipulationen im AG zur Aktivierung frontomedialer Theta-Oszillationen führen, was auf die Verbindung des frontalen Theta mit den exekutiven Gedächtniskomponenten hinweist. Im

Gegensatz dazu wurde die Hypothese, dass Alpha-Oszillationen eine führende Rolle in der Filterung irrelevanter Gedächtnisinhalte spielen, nicht bestätigt. Auch mit den individuellen Unterschieden in AG-Leistung hing die Alpha-Aktivität im EEG nicht zusammen. Statt dessen stellte sich die Aktivität im unteren Beta-Bereich (16-22 Hz) als ein möglicher Faktor heraus, der die individuelle Leistungsfähigkeit im AG mitbeeinflusst. Der Mechanismus dieses Effekts bleibt unklar; eine mögliche Hypothese setzt eine Wirkung der Beta-Oszillationen über eine Aktivierung motorischer Regionen auf die Fähigkeit zu mentalen Manipulationen voraus. Schließlich bestätigen die Ergebnisse dieser Studie die Hypothese, dass die Grenzen der individuellen Fähigkeiten im AG vor allem durch dessen exekutiven Komponenten, vielmehr als von den mit Speicherung und Behalten verbundenen Komponenten, bestimmt werden.

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INTRODUCTION

Human memory is an amazing product of our brains. The memory for facts and skills – what is also called long-term memory – has virtually unlimited capacity. Nevertheless, the unlimited capacity of long-term memory is accompanied by no less fascinating restrictions in how much information we are able to maintain in the scope of memory at a time. Despite a deceptive feeling that we are aware of everything in our environment, we have access to only a small portion of about 4 objects at a time. This immediate memory content that is populating our conscious experience is known as working memory (WM). WM is crucial for many daily tasks such as making a choice from the menu at a restaurant, mentally crossing off an item from a shopping list, or control of the traffic while driving as well as comprehension of this very text.

From the first glance, this bottleneck in the human mind makes no practical sense considering the seemingly great capacity of the brain in other cognitive abilities. Having all the perceived information available in consciousness at the same time seems beneficial. Anyway, the capacity of WM is limited. Furthermore, it is a primary determinant of the individual differences in intellectual abilities. For instance, two meta-analyses and a recent large-scale (N=2200) correlational study found a correlation between WM capacity and fluid intelligence to lie between r=0.71 and r=0.85 (Gignac, 2014; Kane, Hambrick, & Conway, 2005; Oberauer, Schulze, Wilhelm, & Süß, 2005). Therefore, understanding the limiting factors of WM capacity is a major step towards understanding boundaries of human cognitive abilities.

The nature of neural underpinnings of individual differences in WM capacity is an intriguing question interesting both neuroscientists and psychologists. Brain mechanisms underlying individual capacity limits are heavily understudied for the reason of resource demanding psychophysiological research among others. As will be shown in my dissertation only a few studies have attempted to properly touch on this question. Studies of individual differences in psychophysiology are rare. A typical number of subjects of about 20-30 and fewer cannot allow to tackle the problem. The current work sheds some light on the question of what makes people different in their cognitive capacities.

1.1 Working memory

1.1.1 Models of working memory

The term “working memory” was introduced to psychology in 1960 by Miller, Galanter and Pribram (Baddeley, 2003). The authors used a popular analogy of the time of a computer function. The term was later adopted and popularized by Baddeley and Hitch (1974). Baddeley & Hitch’s model of WM is a conceptual successor of another multi-component model of WM developed by Atkinson and Shiffrin (1968) (see Figure 1A). Atkinson and Shiffrin’s model entails a system storing information in three units. The units differ most importantly in the time the information can be stored without being lost completely: (1) sensory register processes information only for a brief period of a few hundred milliseconds, (2) short-term memory (STM) is able to store the information coming from the sensory register as well as from long-term memory in the span of about 15-30 seconds and (3) the last component is long-term memory with no duration limits.

Baddeley & Hitch suggested that STM is more than one unitary storage accommodating all sensory information in one place but comprises different components (see Figure 1C). The three-component model of working memory in its classic formulation consists of separate storage buffers for verbal (phonological loop) and visual (visuospatial sketchpad) content, as well as a central executive. The latter is responsible for maintenance of the active representation of the memory trace, attentional control, active processing and reorganization, or manipulation of information in the sensory buffers. This additional to STM component is what makes WM “working” and differentiates Baddeley & Hitch’s model from the predecessors.

Despite the dominating place of Baddeley & Hitch’s model, alternative models exist. Some of the modern WM models argue that WM is nothing more than an activated part of long-term memory (LTM) (Cowan, 2019; D’Esposito & Postle, 2015; Larocque, Lewis-Peacock, & Postle, 2014; Nee & Jonides, 2013; Oberauer, 2002) (see Figure 1B for Cowan’s model). These models can also be described as state models of WM. The representations in LTM change depending on whether they are in the light of attention or in an inactive passive state out of the attentional spotlight. These models at the first glance may offer a more parsimonious explanation of WM. Nevertheless, there are simple but strong arguments against this explanation (Baddeley, Hitch, & Allen, 2019; Norris, 2017, 2019). First of all, there must be a system that is able to store multiple representations and recall them in the correct order. But this suggests that there must be a separate storage where the order is maintained. Second, activated LTM models are unable to solve “the problem of two”. “The problem of two” refers to the necessity of a system that can represent multiple instances of the same type. For example, if I ask you to remember a sequence of two words, such as dog, dog, how can two identical dogs be activated in LTM at the same time? There should be a system that maintains the order of multiple representations or, in the last example, a number of identical representations. Cowan’s (1999, 2019) response to this critique suggests that there is a system consisting of pointers to LTM that can show what part of the LTM should be active and when, and activated by the pointers parts of LTM. A close look at this system reveals that it is just another name for WM and, therefore, redundant.

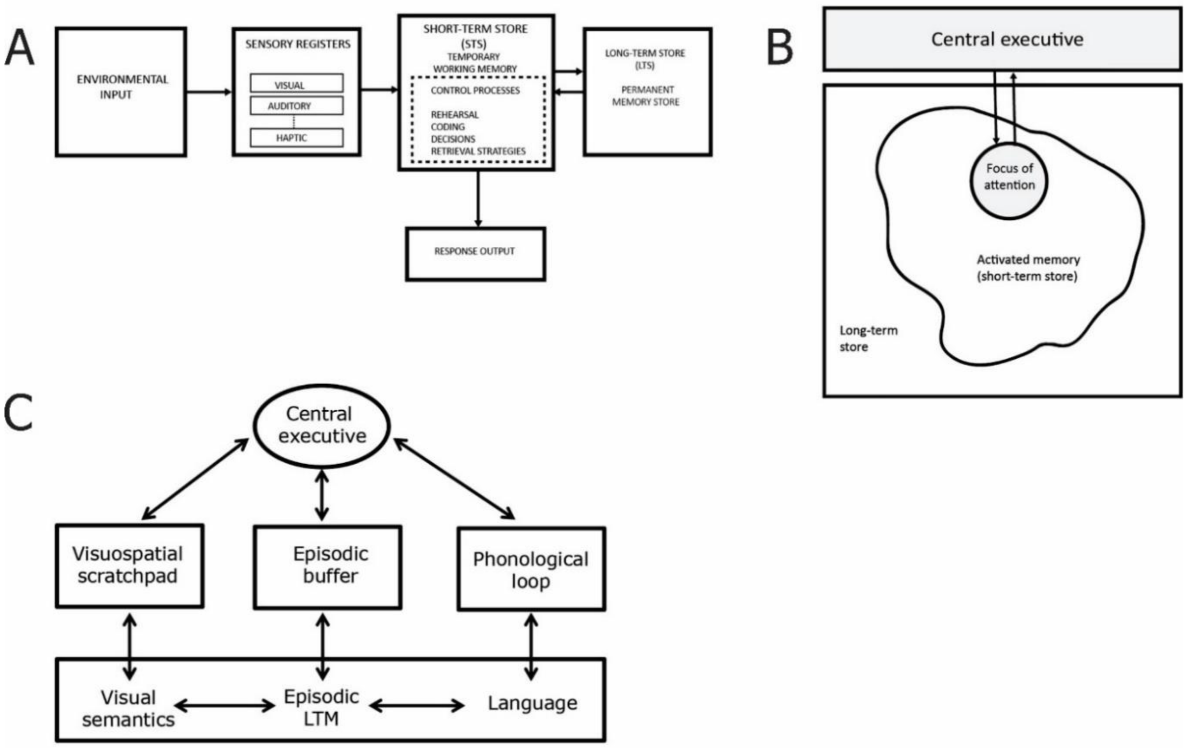

Figure 1 - Models of WM. (A) Atkinson and Shiffrin’s (1968) model (B) Cowan’s (1999) model (C) Baddeley and Hitch’s model (1971) model of STM.

According to different models of WM, temporary storage can be seen as an activated part of LTM or as a separate short-term sensory storage. Either way, in all major WM models storage and attention functions are separated. Understanding the contribution of these two storage-related and attention-related components to individual differences is one of the primary goals of my dissertation. It goes beyond the current work to compare the fitness of different WM models to neural and behavioral data. The operational model used in the course of the manuscript is a simplified multicomponent model of Baddeley & Hitch (1974) with a simple storage component and a central executive as two essential parts of it.

Baddeley (2012) uses the term STM to describe the temporary storage processes or the retention, whereas the term WM is used to refer to the combination of temporary storage and manipulation. In the literature, however, the terms STM (retention) and WM (retention plus manipulation) are often used interchangeably. Moreover, psychophysiological studies often either overtly focus solely on STM or do not distinguish between STM and WM and study STM while calling it WM (Aben, Stapert, & Blokland, 2012). While separation of the two is of paramount importance for the current work, both terms are used in the literature. I will use the term STM, in accordance with Baddeley (2012), when referring solely to the temporary storage components of WM, and the term WM in all other cases.

With a few exceptions most WM tasks in real life require both sensory storage and executive components. For example, keeping a phone number in mind until it is written down or dialed requires transformation of verbal information into a sequence of button presses. The task also involves switching attention between the current number to dial and pressing buttons on the phone panel. A more complex example would be the conversion of a shopping list into the optimal path while shopping. This task, in addition to the translation of the list into a sequence of spatial locations, also involves constant update of information in WM. A simpler example of mental arithmetic even more strongly relies on the ability to manipulate information in WM. The demand on the central executive in these tasks is different but frequently difficult to quantify. In the laboratory setting, however, it is perfectly possible to design such a task where involvement of the executive components of WM would vary in an expected range from being negligibly small to excessively large. Such a manipulation with the tasks' demands would allow to separate different components of WM and to define their impact on individual capacity limits.

1.1.2 Working memory capacity

The limited capacity is a key feature of WM. Three main sources of variance in the WM capacity are most noticeable. First, the number of items to be maintained in WM. Second, the duration of the delay period and the presence of a concurrent task during maintenance of information. Third, individual differences in capacity limits also affect WM performance. In the next sections I will shortly overview the current evidence on sources of WM capacity limits coming from behavioural literature.

1.1.2.1 Tasks to measure WM capacity

In order to measure the WM capacity, a wide range of experimental paradigms is employed. Most of the tasks used in behavioral experimental psychology can be separated into two main categories: simple span tasks to measure STM and complex span tasks to measure WM (Aben et al., 2012). The most commonly used simple span tasks are word, letter and digit span tasks. The idea of these tasks is to give the participant a list of to-be-remembered items (words, digits, letters, etc.) and after a short period of encoding and sometimes delay to ask the participant to recall the items either freely (free recall) or in the order they were presented (serial recall). All these tasks involve only retention of the items. In complex span tasks after encoding the presented item(s), the participant is presented with another concurrent task that occupies the delay period partially or completely. For example, the participant in the operation span task is required to solve arithmetical problems while maintaining the encoded information. A version of the reading span task would require the participants to read sentences aloud and memorize the last words in these sentences. Complex span tasks are considered to be WM tasks as opposed to simple span which are STM tasks.

The original purpose of complex span tasks was to ensure that both storage and executive components of WM are engaged because capacity measures in this type of task are closer to real-life activities such as reading and math. However, the additional activity introduced in operation span and reading span is simply a distractor. The role of the central executive here is to protect WM content from the distractors. More ecologically valid task involves manipulation with the content that is already present in STM. This category of complex span tasks is known under the term transformation span tasks. Two noticeable examples of transformation span tasks are backward span and alpha span tasks. The tasks involve encoding a string of letters and then recalling them in alphabetical order in alpha span or in the reverse order (rather than in the presentation order) in the backward span task. Transformation span tasks require that the processing is executed during retrieval, which limits their utility in EEG research. However, modifications of transformation span tasks have been successfully used in psychophysiological research (e.g., Berger et al., 2014; D'Esposito et al., 1999; Griesmayr et al., 2014).

It has to be stressed that none of the above mentioned, or any other WM/STM tasks, are process-pure (Conway et al., 2005). All of them entail a combination of retention and manipulation processes but with a different extent in simple and complex span tasks.

1.1.2.2 Set-size (load effect)

The accuracy in WM tasks declines with an increasing number of items to be remembered (Luck & Vogel, 1997; Miller, 1956). This effect has been known as the effect of memory set size or of memory load. The memory load effect is a reflection of the WM capacity limit. Originally proposed by Miller (1956) 7 ± 2 capacity limit was later reconsidered by (Cowan, 2001) who gave an estimation of a typical WM capacity limit to be 4 items. However, the 4 items limit refers to a condition when rehearsal and chunking are restricted. When rehearsal of verbal material such as digits or letters is not blocked, then capacity limit reaches the number of items an individual can rehearse in about 2 s (Baddeley, 1996; Cowan, 2001). The capacity increases further if chunking is possible. Thus, the task to encode a string of 9 digits is feasible because the string is automatically converted into 3 three-digit numbers. Therefore, the set-sizes above 4 items, as frequently used in verbal WM research, do not demand beyond average WM capacity.

The difference between Miller's and Cowan's estimations of capacity limit is primarily the matter of definition. The limit is defined as a level of load when the accuracy drops below a certain threshold. The classic definition of memory span, as the number of items that a person can reproduce in 50% of the trials, yields the capacity limit close to Miller's 7 ± 2. When it is defined as the number of items when the accuracy is perfect or virtually error free, then the limit of 4 items is obtained (Oberauer et al., 2018).

1.1.2.3 Delay duration and processing demands

The accuracy is lower in complex span tasks than in simple span tasks (Shipstead, Lindsey, Marshall, & Engle, 2014). Representations in WM are vulnerable when a concurrent task is introduced. The performance of the concurrent task facilitates forgetting. Forgetting in complex span tasks is determined by the proportion of time spent on the secondary distracting task. It implies that the longer the attention is occupied by the concurrent task, the stronger decline in WM performance is observed (Barrouillet, Bernardin, Portrat, Vergauwe, & Camos, 2007).

Distracting activity during delay period typically prevents rehearsal. The level of performance disruption correlates positively with the duration of the delay. When the distracting task involves constantly-changing materials such as counting backwards, the performance drops in the first 15-18 s. After 18 s of distracting activity the performance does not decline further, which is known as the Brown-Peterson effect (Brown, 1958; Peterson & Peterson, 1959). Increasing duration of the delay period negatively affects WM performance in most cases (Ricker & Cowan, 2010; Ricker, Spiegel, & Cowan, 2014). However, the duration of the delay in verbal WM tasks does not affect performance when rehearsal is not suppressed (Oberauer, Farrell, Jarrold, & Lewandowsky, 2016; Oberauer et al., 2018).

1.1.2.4 Individual differences

Individual differences in WM performance positively correlate with performance in the attention capture tasks (Engle, 2002; Fukuda & Vogel, 2011; Kane, Conway, Hambrick, & Engle, 2008; Unsworth & Spillers, 2010). In this type of tasks salient but goal-irrelevant stimuli capture attention but are required to be ignored. Attention capture tasks do not load temporary storage components of WM and the individual differences in these tasks can be explained on the basis of differences in executive control (Shipstead et al., 2014). As proposed by Engle (2002) individual differences in WM capacity are not limited by sensory storage capacity alone but depends on the ability to control attention.

The developers of the reading span task Daneman and Carpenter (1980) found that scores in their task were a better predictor of reading comprehension than the simple span task. Since then, a number of studies has aimed to examine individual differences in WM with a relation to higher order cognitive abilities. For this sake, researchers employ factor analysis, which looks for latent variables to explain the contribution of different sources of variance to individual differences. Thus, a study showed that WM capacity but not STM capacity is a good predictor of general intelligence (Conway, Cowan, Bunting, Therriault, & Minkoff, 2002). This finding may suggest that variation in WM capacity has larger contribution to higher order cognitive abilities than STM capacity.

1.2 Electrophysiological correlates of working memory

Electroencephalography (EEG) is a broadly used method in psychology. The EEG allows to non-invasively measure electrical potentials in the cortex. Moreover, the EEG can reveal temporal subprocesses underlying WM. Behavioral measures such as reaction time (RT) and accuracy only reflect the result of information processing in WM. Dissecting the temporal structure of WM using behavioral measures as well as other popular neuroscientific tools such as functional magnetic resonance imaging (fMRI) is compounded with a lot of assumptions and limitations (Gitelman, Penny, Ashburner, & Friston, 2003; Lindquist, Meng Loh, Atlas, & Wager, 2009; Steinbrink et al., 2006). fMRI studies of WM are focused on spatial distribution of activation in the brain and have limited time resolution. Qualitatively different types of information about WM is available from EEG signal. Multidimensional EEG data can provide insights to test hypothesis on models of WM. For example, if distinct neural patterns are observed during the presence of different WM phenomena, this may suggest that such phenomena are dissociable and should be treated as distinct elements of the WM model. Owing to the perfect time resolution, the method is able to improve our understanding of neural account for short-time living psychological processes.

There is a number of methods to derive information from the EEG signal. In my dissertation I will use two of them: time-frequency analysis and event-related potentials (ERPs). In short, averaging of EEG traces in the time domain will get insight of event-related short-term changes in the voltage between two EEG electrodes (Luck, 2014). Exploring the EEG signal in the frequency domain will reveal activation and suppression of brain oscillatory activity over time (Pfurtscheller & Da Silva, 1999).

1.2.1 Event-related brain potentials

1.2.1.1 P300

An ERP waveform is typically seen as a sequence of components related to the stages of sensory and cognitive processing of information as well as motor preparation and response execution. The most prominent ERP component frequently studied in verbal WM research is P300. There is more than one peak typically called P300. P3a and P3b are the members of the so called late positive complex – a set of positive deflections with roughly 200-500 peak latency. The late positive complex is frequently associated with cognitive stimulus processing (Polich, 2007). The second P300 peak (P3b) with a parietal distribution is found to be closely related to WM processes.

A variation of verbal WM Sternberg task (Sternberg, 1966, see 1.2.2.2 section and Figure 3 for detail) was used in the current study. Encoding, maintenance and retrieval temporal subprocesses are disentangled in the Sternberg task. Verbal WM research by means of this task employs both P3b to stimuli in the encoding phase and to the retrieval of WM content. In the course of the manuscript, I will use the terms *encoding P3b* and *retrieval P3b*. The encoding P3b is a subcomponent of the late positive complex to the presentation of the WM items that should be memorized. The retrieval P3b is a part of the response to the one-item probe.

An influential hypothesis of the nature of P3b postulates that this component is a reflection of updating the content in WM (e.g,, Polich, 2007). According to the hypothesis the amount of processing required by the stimulus increases the amplitude of P3b (Donchin & Coles, 1988). The direct relationship between P3b and memory finds support in the effect of larger encoding P3b to the better recalled items (Fabiani, Karis, & Donchin, 1986; Karis, Fabiani, & Donchin, 1984; Rushby, Barry, & Johnstone, 2002). But this effect relates P3b to long-term, rather than short-term, memory. According to another interpretation, P3b may index allocation of attentional resources to information processing (Kok, 2001; Polich, 2007). Attention is a limited resource. Within this framework, an increase in cognitive processing demands reduces P3b amplitude (Kok, 2001).

Following this logic, allocation of resources to encode the information into WM storage would be expected to decrease P3b with increasing load. However, encoding P3b literature is scarce in support for this hypothesis. Apparently similar experimental paradigms frequently led to rather different outcomes. Sometimes encoding P3b did not responded to the increasing load at all (Ruchkin, Johnson, Canoune, & Ritter, 1990). Contradicting the expectation, an increase of WM load subsequently increased the amplitude of encoding P3b in a number of studies (Getzmann, Wascher, & Schneider, 2018; Gomarus, Althaus, Wijers, & Minderaa, 2006; Houlihan, Stelmack, & Campbell, 1998; Speer & Soldan, 2015). Furthermore, Grune et al. (1996) found that increasing WM load led to a decrease of P3b but the effect reached a plateau at 4 items. Saturation of P3b when the set-size exceeded 4 items was also demonstrated in another study (Scharinger, Soutschek, Schubert, & Gerjets, 2017).

Numerous verbal WM studies demonstrated a decrease of retrieval P3b with increasing load in the Sternberg or similar tasks (Golob & Starr, 2004; Jung et al., 2015; Kim et al., 2014; Lefebvre, Marchand, Eskes, & Connolly, 2005; Lorist, Snel, Mulder, & Kok, 1995; Marsh, 1975; Pelosi, Hayward, & Blumhardt, 1995). In the n-back paradigm (see 1.2.2.2 section and Figure 3 for detail on the task), where encoding and retrieval P3b are intersected, the same effect of P3b attenuation with an increasing load was repeatedly observed (Bailey, Mlynarczyk, & West, 2016; McEvoy, Smith, & Gevins, 1998; Watter, Geffen, & Geffen, 2001; West, Bowry, & Krompinger, 2006).

Summarizing 20th century literature, Kok (2001) suggested that the amplitude of P3b depends on the amount of resources or effort allocated to the task (Kok, 2001). Task difficulty is related to the cognitive capacity to perform the task. When the WM capacity is high, an increase in task difficulty does not require the same effort as if the capacity is low. The relationship between P3b and WM capacity rarely became a subject of investigation. P3b amplitude was found to be larger in high performers than low performers in an n-back task in two studies (Dong, Reder, Yao, Liu, & Chen, 2015; Morrison, Kamal, & Taler, 2019). A more complex relationship was reported by Daffner et al. (2011): P3b increased with load in the high performance group and decreased in the low performance one. Moreover, in a verbal WM study encoding P3b was larger in the high-performance group (Wiegand et al., 2016). These observations make P3b an interesting target to explore individual differences in WM.

As will be discussed in the next sections in detail, small sample sizes in individual differences studies are rather a norm in the field. For example, in the 4 studies reviewed above, Morrison et al. based their conclusion on a sample of 22 high / 17 low performance individuals. In Daffner et al., Dong et al. and Wiegand et al. sample sizes in two groups were 12/11, 14/14 and 8/8 respectively. The low statistical power of these studies may well be a factor yielding contradictory data.

1.2.1.2 Event-related slow potentials

Slow direct current drifts with a larger time constant than typical for shorter latency ERPs such as P300 have been shown to be related with cognitive processing (Birbaumer, Elbert, Canavan, & Rockstroh, 1990). These slow components of ERPs are known under different names when studied in different contexts.

One of the most prominent slow ERP is the contingent negative variation (CNV). CNV is a slow negative potential observed during anticipation of an event. The wave was first described by Grey Walter in 1964 (Walter, Cooper, Aldridge, McCallum, & Winter, 1964). In the classical experiment one stimulus (warning, S1) after multiple pairings becomes predictive to another one requiring motor response (imperative, S2). It is believed that CNV reflects the integration processes of sensory information and the preparation of the response (Birbaumer et al., 1990). CNV has a fronto-central scalp distribution and generators covering the motor and prefrontal cortex, and the basal ganglia (Bareš & Rektor, 2001; Basile, Ballester, de Castro, & Gattaz, 2002; Gómez, Marco, & Grau, 2003).

In the n-back paradigm CNV was found to be sensitive to manipulations with task complexity (Gevins et al., 1996; McEvoy et al., 1998). CNV was shown to decrease (became less negative) as a result of an increasing WM load (Gevins et al., 1996; McEvoy et al., 1998). CNV studies utilizing the Sternberg task are less common and mainly conducted during the first rise of ERP research in the 1970's. In these studies CNV was shown to respond to the experimental manipulations with a WM load (Ford, Roth, Mohs, Hopkins, & Kopell, 1979; Roth et al., 1975; Roth, Rothbart, & Kopell, 1978). The researchers asked participants to memorize sequentially presented digits and) to retain the digits in WM after a warning tone (S1) for about one second until the probe (S2) was presented. These studies yielded the same result: CNV was smaller in the higher WM load condition. The conclusion finds support in the other works of similar age (Tecce, Cattanach, Yrchik, Meinbresse, & Dessonville, 1982; Tecce, Savignano-

Bowman, & Meinbresse, 1976). This finding implicates that the division of attentional resources in a WM task attenuates CNV.

Contrary to CNV findings, Ruchkin and colleagues decisively demonstrated a WM load related effect of increasing amplitude of a slow wave (Ruchkin, Canoune, Johnson, & Ritter, 1995; Ruchkin et al., 1994, 1990; Ruchkin, Johnson, Grafman, Canoune, & Ritter, 1992). This slow wave mainly covered frontal cortical areas. The effect was memory specific and did not appear in a visual search or attention tasks (Ruchkin et al., 1990). It was characterized by left frontal topographical distribution in the verbal tasks and localized in posterior areas in the visual-spatial tasks (Ruchkin et al., 1999, 1994, 1992; Ruchkin, Berndt, et al., 1997; Ruchkin, Johnson, Grafman, Canoune, & Ritter, 1997). Moreover, in one the studies Ruchkin et al. (1995) demonstrated a clear difference between CNV reflecting mainly expectation and preparation to the motor response, and the memory related slow cortical potentials (SCP) discovered by Ruchkin.

SCP are thought to originate from superficial cortical layers (Hinterberger et al., 2003; Khader, Schicke, Röder, & Rösler, 2008; McCallum & Curry, 2013). Negative SCP shifts are correlated with the depolarization of cortical neurons and, therefore, with a decrease of their excitation threshold. Moreover, SCP were found to correlate with fMRI blood-oxygen-level-dependent (BOLD) signal (Khader et al. 2008). Thus, despite having low spatial resolution, SCP can be seen as an electrophysiological representation of brain metabolism.

Starting from the initial report by Luck and Vogel (1997), the change detection paradigm has become one of the main tools to study WM in neuroscience (see Figure 2A). In this paradigm a set of items (most frequently colored squares) is presented simultaneously for a short period time (typically 100-500 ms). After a brief delay (typically 800-1100 ms) another, either identical or different, set of the same size is presented asking the participant to decide whether the set has changed or remained unaltered. As a development of Luck and Vogel’s paradigm, the lateralized change detection task was created (Vogel & Machizawa, 2004) (see Figure 2B). The cue instructing to attend one of the hemifields appears before the presentation of the memory array. Direction of attention to only one side of the display facilitates the generation of another slow ERP. Contralateral delay activity (CDA) is a sustained slow negative potential over posterior electrodes more negative in the contralateral to the attended side stimuli. In the first work by Vogel and Machizawa and in numerous replications CDA was found to be sensitive to the number of items in WM (for a review see Luria et al., 2016). The simplicity of the task and the good reproducibility of the phenomenon have made this paradigm one of the most frequently used in modern WM research.

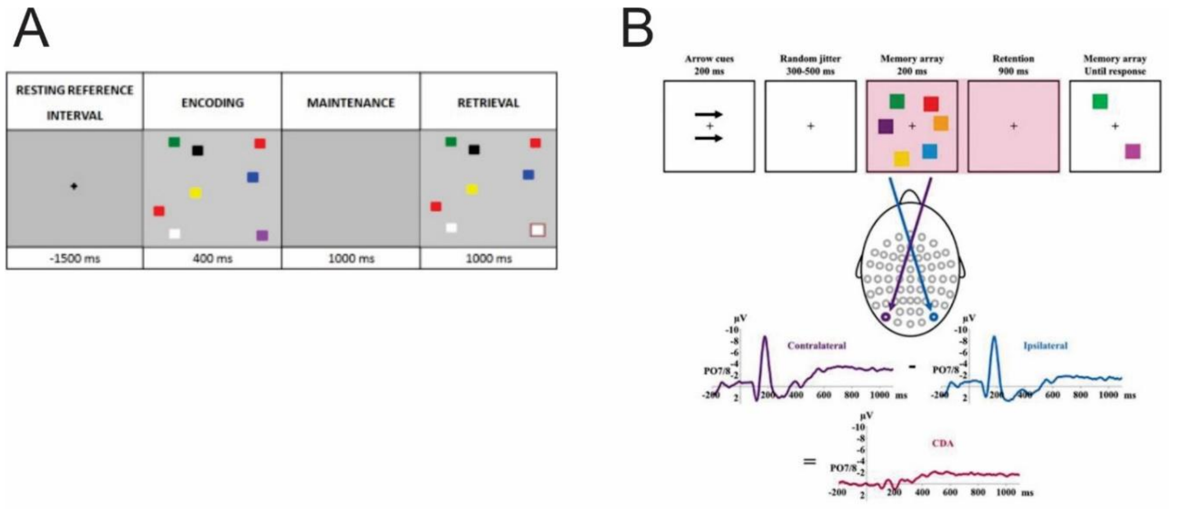

Figure 2 – (A) Change detection paradigm by Luck and Vogel (1997) (B) Lateralized change detection task and CDA waveforms (adopted from Luria et al. (2016) with permission from Elsevier)

CDA share similar features with the SCP reported by Ruchkin. CDA is also a slow component spreading over at least a few hundred milliseconds. It becomes more negative with an increasing set-size. At the same time, a number of differences exist. In contrast to Ruchkin's SCP, CDA increases up to individual WM capacity. This number is close to 4 if the capacity is calculated according to Cowan's definition[1] of visual WM capacity (Cowan, 2001). This formula is frequently used in studies employing Vogel's change detection paradigm but almost completely neglected in verbal WM studies. Ruchkin never used the formula but set-sizes in his studies typically exceed the limit of 4 but continue increasing SCP amplitude. However, in a more recent study the SCP reached plateau at 3 items (Liu et al., 2018).

Another difference between CDA and SCP is the spatial distribution. CDA is almost solely present in posterior leads whereas SCP cover the whole scalp with stronger

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[1] The formula is as follows K = S x (H - F), where K is WM capacity, S is the set-size, H is the observed hit rate (correct response when one item in the array changed) and F is the false alarm rate (incorrect response when there was no change in the array).

effects in fronto-central areas. This is the case not only in typical for this task visual WM but also in a verbal version of the task with letters used instead of the colored squares (Predovan et al., 2009; Prime, Dell'acqua, Arguin, Gosselin, & Jolicoeur, 2011; Prime & Jolicoeur, 2010; Rajsic, Burton, & Woodman, 2019; Wiegand et al., 2014).

The typical duration of the delay period in the change detection paradigm varies between 800 and 1000 ms. As an exclusion, Drew, Horowitz, Wolfe, & Vogel (2011) used 1500 ms delay period. As can be seen in their Figures the CDA amplitude returned to the baseline level after about 1000 ms. In Fukuda et al. (2015) the retention interval was increased to 4000 ms. Pushing delay beyond normal for this paradigm value of 800 ms confirmed that CDA disappeared 1000 ms after the stimulus onset. In contrast to CDA, SCP is persistent over the whole delay period.

The SCP can be studied in a regular task such as the Sternberg paradigm. Moreover, due to the clear relationship between the SCP and verbal WM load Ruchkin suggested that this negative ERP component is associated with rehearsal processes inside the phonological loop (Ruchkin et al., 1999, 1992). It makes the SCP a potential marker for testing the role of phonological loop in individual differences in WM. However, there are only a small number of studies employing SCP to study individual differences in WM. Thus, one study found that a left frontal SCP differentiate between individuals with low (N=8) and high (N=8) WM span with more negative values correlating with better scores (Münte, Schiltz, & Kutas, 1998).

1.2.2 Oscillatory brain activity

Event-related potentials including slow cortical potentials is an important technique to study WM but the main focus of the current work is on brain oscillations. In the next sections I shall, first, give a short overview of brain rhythms and their significance in a broader context of cognitive neuroscience and psychology. Second, I shall present the results of a comprehensive systematic review on the oscillatory correlates of WM.

1.2.2.1 Brain rhythms

The oscillations play an important role in human cognition and represent an energy efficient mechanism for communication within the brain (Buzsaki, 2004; Fell & Axmacher, 2011). Oscillatory brain activity is usually categorized into five frequency bands or rhythms: delta (0.5-4 Hz), theta (4-8 Hz), alpha (8-13 Hz), beta (13-30 Hz also frequently subdivided into lower beta: 13-20 Hz, and upper beta: 20-30 Hz), and gamma (> 30 Hz). An important question of modern neuroscience is whether different frequencies serve different distinguishable purposes in the brain and whether they can be mapped on different cognitive functions and aspects of behavior.

Since the seminal work by Hans Berger in 1929 (Berger, 1929), human EEG has become a part of the scientific enterprise. The brain waves with frequencies between 8 and 12 Hz were termed alpha as they were first discovered. Since then, the alpha rhythm has been the main focus of interest in the EEG community. Alpha activity has been linked to attentional processes (Benedek, Schickel, Jauk, Fink, & Neubauer, 2014; Klimesch, Sauseng, & Hanslmayr, 2007), long-term (Hanslmayr, Spitzer, & Bäuml, 2009) and short-term memory (Klimesch, Freunberger, & Sauseng, 2010), emotions (Aftanas & Golocheikine, 2001), consciousness (Engemann et al., 2018) and other functions.

Alpha rhythm is strong when brain regions are inactive. The effect of alpha suppression with eyes opening, first observed by Berger, led to formulation of the hypothesis that alpha rhythm represents cortical idling (Pfurtscheller, Stancak, & Neuper, 1996). This hypothesis postulates that an event-related alpha attenuation reflects activation of the underlying brain areas. More modern view sees the role of alpha oscillations in functional inhibition of specific brain regions to block information transfer to task-irrelevant areas of the brain (Jensen & Mazaheri, 2010). Spectral power of alpha activity in a certain cortical region is reduced by appropriate sensory stimulation (e.g. a flash of light would suppress alpha in occipital regions of the brain) (de Vries, Driel, & Olivers, 2017; Durup & Fessard, 1935; van Ede, de Lange, Jensen, & Maris, 2011). Directing attention to a part of the sensory space generates similar effect of alpha suppression. For example, alpha in the right hemisphere is suppressed by attending to the left visual hemifield (Fukuda et al., 2015; Sauseng et al., 2009).

Theta rhythm (4-8 Hz) is not a unitary phenomenon. There is a theta rhythm observed during sleep; a theta rhythm recorded directly from hippocampus in animals and human patients; a theta rhythm covering posterior cortex in the resting state; and a theta rhythm peaking in frontal midline EEG channels. Although nobody has compared all the thetas in a single study, they probably represent different processes (Mitchell, McNaughton, Flanagan, & Kirk, 2008). The most relevant to the current work theta is frontal midline theta (FMT) rhythm. In the rest of the manuscript any mention of theta rhythm or FMT will refer to frontal midline theta unless stated otherwise. Initially, Ishihara & Yoshii (1972) observed a boost in the power of oscillations around 6.5 Hz at the Fz lead during performance of numerous cognitive tasks (mostly involved mental arithmetic). The FMT power increase was associated with a variety of cognitive processes such as sustained attention, episodic and working memory, executive control and emotions (Aftanas & Golocheikine, 2001; Klimesch, 1999; Nigbur, Ivanova, & Stürmer, 2011; Nyhus & Curran, 2010; Sauseng, Hoppe, Klimesch, Gerloff, & Hummel, 2007).

Source modeling based on EEG and magnetoencephalography (MEG) identified possible sources of FMT in the anterior cingulate (ACC) and medial prefrontal cortex (Gevins, Smith, McEvoy, & Yu, 1997; Ishii et al., 1999; Meltzer, Negishi, Mayes, & Constable, 2007; Onton, Delorme, & Makeig, 2005). Furthermore, theta activity correlated with glucose metabolism in the ACC acquired by the means of positron emission tomography (PET) (Pizzagalli, Oakes, & Davidson, 2003). On the other hand, a number of concurrent EEG-fMRI studies demonstrated negative correlation between the FMT amplitude and BOLD response in the ACC and medial prefrontal cortex (Meltzer et al., 2007; Michels et al., 2010; Michels, Lüchinger, Koenig, Martin, & Brandeis, 2012; Mizuhara, Wang, Kobayashi, & Yamaguchi, 2004; Scheeringa et al., 2008, 2009; White et al., 2013). These negative correlations between low frequency oscillations and BOLD signals may seem unexpected, given a well-known finding of Logothetis et al. (2001) showing a positive correlation between local field potentials and BOLD signal. However, Logothetis et al.'s finding accounts for broad band oscillatory activity (10–130 Hz) without separation into specific rhythms. This probably means that the relationship between different frequency bands and metabolic activity is not uniform. It is possible that FMT increase is indeed an index of inhibitory activity in the ACC and adjacent areas. BOLD response may also be not a direct reflection of information processing coordinated by oscillatory brain activity. The exact nature of the role of FMT in cognition remains to be elucidated. Nevertheless, directly tagging an increase in FMT as activation of the ACC may not be fully justified.

The activity of beta frequency band (13-30 Hz) has been traditionally linked to sensorimotor cortex (Pfurtscheller, Brunner, Schlögl, & Lopes da Silva, 2006;

Pfurtscheller & Neuper, 1997). Beta activity tends to be suppressed in preparation or execution of a movement, motor imagery, in response to tactile stimulation or expectation of it (Pavlov & Kotchoubey, 2019; Pfurtscheller & Neuper, 1997; Spitzer, Wacker, & Blankenburg, 2010; van Ede et al., 2011). Beyond its role in the sensorimotor processing, beta activity has been sporadically reported to be involved in a number of cognitive operations such as language (Weiss & Mueller, 2012), long-term memory (Hanslmayr et al., 2009), visual perception (Kloosterman et al., 2014) and many others (Engel & Fries, 2010; Spitzer & Haegens, 2017). Suppression as well as enhancement of the upper (20-30 Hz) and lower (13-20 Hz) beta rhythms correlated with the involvement in cognitive processing (Hanslmayr et al., 2009; Leiberg, Lutzenberger, & Kaiser, 2006; Pavlov & Kotchoubey, 2017; Tallon-Baudry, Bertrand, Peronnet, & Pernier, 1998). The relationship between beta activity and brain metabolism as well as neuronal firing rate is unclear. Thus, Whittingstall & Logothetis (2009) found no correlation between the spike rate and beta band activity in monkeys. A small number of human EEG-fMRI studies focusing on beta activity do not provide a conclusive answer about the relationship between beta oscillations and BOLD signal (for a review Spitzer & Haegens, 2017). Generally, a coherent picture on the role of beta in cognition is far from being complete. In the realm of WM research, the functional role of beta seems to be least understood.

Gamma rhythm is defined as oscillatory brain activity with frequencies higher than 30 Hz. In a number of studies evoked gamma activity increased in response to sensory and cognitive stimulation (Herrmann, Fründ, & Lenz, 2010). Increase of gamma activity may reflect engagement of local neural populations into the task performance (Lachaux, Axmacher, Mormann, Halgren, & Crone, 2012). Even though intracranial EEG (iEEG) and MEG repeatedly demonstrated robustness of gamma responses in cognitive tasks (Herrmann et al., 2010; Jerbi et al., 2009), gamma obtained from the EEG signal may be less robust. The reason for this is a strong contamination of EEG by muscle artifacts mainly occupying higher frequencies such as gamma frequency band (Muthukumaraswamy, 2013).

Delta rhythm occupies the other end of the EEG spectrum. Delta activity is ranging between 0.5 and 4 Hz. Current views attribute a minor role in cognition to delta rhythm in wakefulness. Brain activity displays a 1/f-like spectral pattern making slow oscillations such as delta rhythm the largest contributor to the power spectra (He, 2014; Pritchard, 1992). Delta frequency band is heavily contaminated by movement and other physiological artifacts such as ocular activity and skin potentials. Acquisition of a clean signal in the delta band during wakefulness is a difficult task. On the contrary, delta activity during sleep plays a tremendous role in consolidation of memory (Diekelmann & Born, 2010). However, the role of oscillations in other states different from wakefulness is going beyond the scope of my dissertation.

Given the limitations of studying gamma and delta activity by means of EEG I will dedicate only limited attention to them in the systematic review.

1.2.2.2 Experimental paradigms to study the role of oscillations in WM

Some experimental paradigms employed in the behavioral studies of WM are more suitable for EEG research than others. Normally in behavioral WM studies only the result of cognitive processing (e.g. RT or accuracy) is a subject of analysis. Unlike the behavioral outcomes data, by means of EEG we are able to quantify brain activity 1000 times a second. This advancement enables us to follow the progression of cognitive operations on a fine time scale. However, EEG is susceptible to artifacts of different nature. The necessity to minimize movement and ocular artifacts during EEG recording creates additional constraints on how WM tasks are designed. There is a number of key features of a good task meant to be used while recording brain activity. Among others, a clear separation of the events in the task helps to avoid overlap of the underlying cognitive processing stages. Usage of a fixation cross helps to minimize ocular activity and to create a reference time interval. The properties of the tasks also depend on the WM sensory modality. The main focus of the current work is verbal WM and I will introduce the most common tasks used in verbal WM studies.

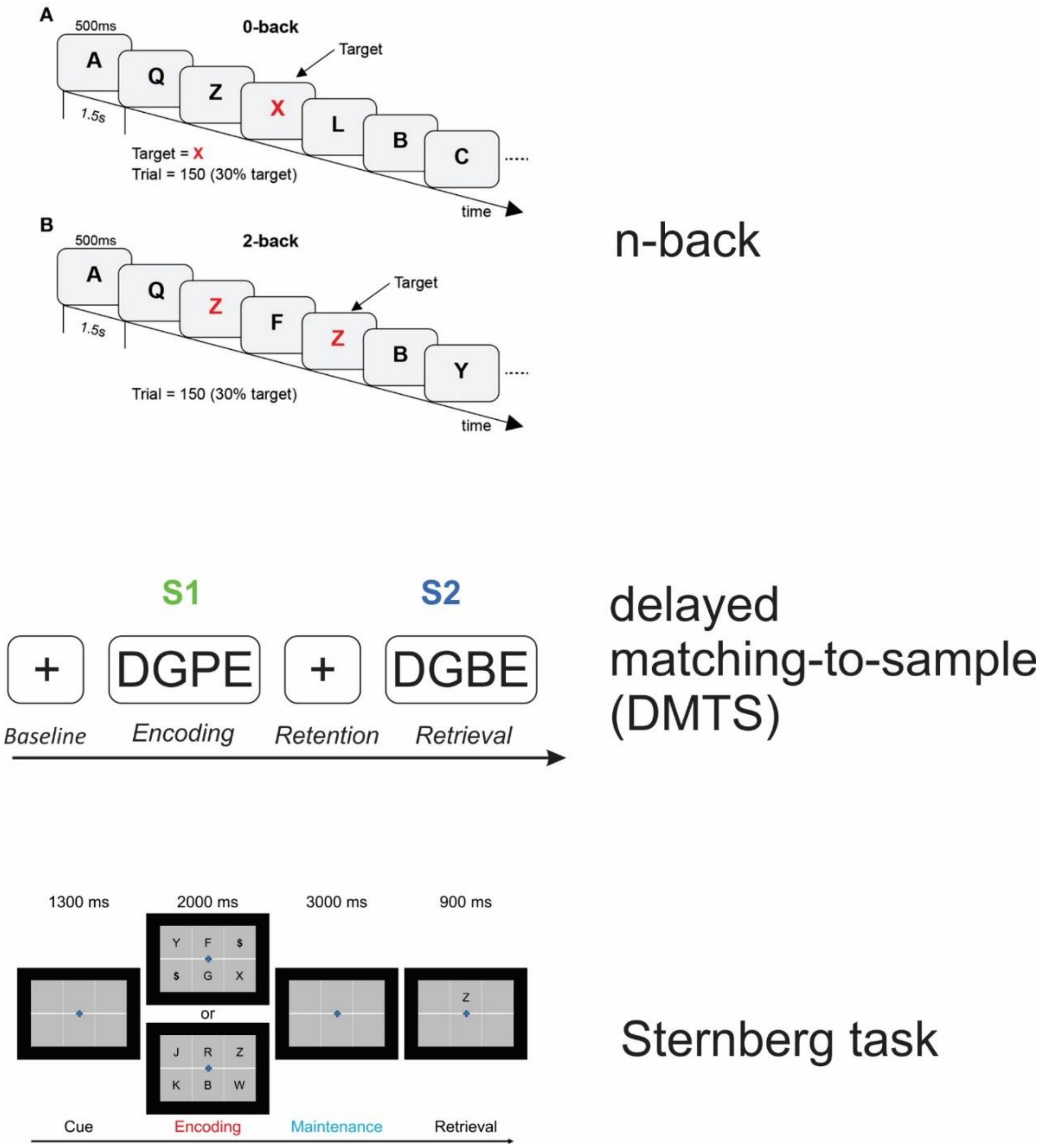

Figure 3 – Typical WM tasks used in verbal EEG studies. Notes: N-back task adapted from Dai et al. (2017). Sternberg task adapted from Proskovec, Heinrichs-Graham, et al. (2019) with permission from Elsevier

Among verbal WM tasks. the n-back task is one of the most frequently used. In a visual n-back task a continuous sequence of items (e.g. letters or digits) is presented to the participant. At the presentation of each display the participant makes the decision by a button press whether the item in the current display matches the item presented N displays back (see Figure 3). Thus, in the 1-back task the participant has to compare the stimulus being currently on the screen and the previously presented stimulus stored in memory, and press the button if the two are identical.

In the n-back task memory-related brain activity is confounded with the activity related to the motor response. Therefore, the results of the time-frequency analysis obtained in studies employing this paradigm are likely to be biased. Alpha/beta activity related to the preparation to the response and the rebound after its execution is mixed with the activity related to the maintenance of information in WM and decision making (Pesonen, Hämäläinen, & Krause, 2007). For instance, Chen & Huang (2015) reported a significant effect of WM load on the activity in the beta frequency band. However, the difference in the onset of beta activity between 1-back and 2-back conditions was the same as the difference in reaction time between the two conditions. Beta suppression latency in the n-back task correlated with reaction time in another study (Palomaki, Kivikangas, Alafuzoff, Hakala, & Krause, 2012). Therefore, the effect observed by the authors is more likely to be related to the execution of the response than to the WM performance. Even using longer inter-stimulus intervals (ISI) as in Deiber et al. (2007) (3.5 s) does not protect from the rebound of alpha-beta activity after the response. Even if no response trials are analyzed, the EEG activity may be contaminated by the response suppression. Moreover, retention and manipulation components of WM are overlapped and not distinguishable in this task. The difficulty in isolation of directly WM related cognitive operations makes the task hardly suitable for EEG.

Many neuroscientific studies of WM employ delayed matching-to-sample task (DMTS) (see Figure 3). Technically speaking, this task is a more common name for the change detection paradigm described in previous sections (Luck & Vogel, 1997). Perhaps, the main difference is typically longer delay periods in DMTS. The task allows to separate temporal subprocesses in WM such as encoding, maintenance and retrieval. DMTS shares this advantage with the most popular task in verbal WM research – the Sternberg task (Sternberg, 1966) (see Figure 3). The encoding and maintenance phases are identical to DMTS but a single-item probe is used at the retrieval stage. The task requirement for the participants is the same – to decide whether the probe matches any of the items in the encoded memory set. Unlike DMTS, the stimuli in the Sternberg task can be presented either simultaneously or successively. It may help to further increase temporal resolution of the task by comparing brain activity after encoding of successive memory items.

Modifications of DMTS and Sternberg were shown to be a useful basis to develop WM paradigms involving manipulations of information in WM. As will be shown in the systematic review of the literature in the next section, genuine WM tasks or tasks with manipulations are particularly rare in the field of EEG research.

1.2.2.3 Systematic review protocol

Typically, in narrative reviews the data are selectively reported in the way when only most visible and/or supporting the narrative studies are referenced (Bushman & Wells, 2001; Pae, 2015). It seems to be especially true for the introduction sections of research articles. The area of EEG correlates of WM is not an exclusion. A number of narratives exists (Klimesch, 1999; Roux & Uhlhaas, 2014; van Ede, 2018). Systematic reviews on this topic are lacking. I believe that before any substantial progress in the field can be made, a comprehensive and unbiased inventory of the current findings has to be done. From the first glance, the amount of the literature on oscillatory mechanisms supporting WM performance is enormous. This is probably the reason why up to date there has been no attempts to write a systematic review on this wide topic. The following sections will, first, describe the methodology of the conducted work.

1.2.2.3.1 Objectives

The main objective of the review was to systematically study oscillatory activity during maintenance of verbal information in WM in healthy young individuals under normal conditions.

The following research questions are formulated to achieve this goal:

1. How do manipulations with WM load affect EEG activity?
2. How are different components of WM represented in the EEG?
3. What are the effects of delay period duration on the EEG?
4. How do individual differences in WM performance influence the EEG?

1.2.2.3.2 Search strategy

Following PRISMA statement (Moher, Liberati, Tetzlaff, & Altman, 2009) two databases (Pubmed and Web of Science) were included in the search.

(eeg OR electroencephalography OR electrophysiolog*) AND ((working memory) OR (short-term memory)) query was used on 22.04.2019

1.2.2.3.3 Screening on eligibility criteria abstracts/titles

Inclusion criteria:

1. EEG study
2. human subjects
3. study oscillatory activity
4. population of healthy young adults

Exclusion criteria:

1. animal research
2. ERP study
3. MEG or iEEG study
4. special population (such as children, elderly, patients, etc)
5. substance use (alcohol, caffeine, nicotine consumption or other drugs)
6. motor memory task (e.g. sequential motor task)
7. simulation or methods paper
8. review, editorial, letter to the editor
9. stimulation studies (tES, TMS)
10. interventional study (e.g., influence of physical exercise)
11. studies with real life concurrent tasks (e.g., driving, flight simulator, jogging, cycling)

1.2.2.3.4 Full texts screening

The inclusion/exclusion criteria were refined to satisfy the objective to study oscillatory activity during maintenance of verbal information in WM. Another inclusion criterion that was difficult to infer from the abstracts was the type of analysis. Only those studies were included where spectral power was calculated and statistical output was reported. If one article comprised multiple experiments in different samples, they were treated as independent records. In the opposite situation, if an article used the dataset reported in another article, the record was excluded. The articles, in which delay period was not analyzed statistically but at least 1 sec of visual representation of spectral power during delay was presented, were included into the review as well.

Inclusion criteria:

1. the task should follow the model with a separate delay interval
2. the duration of the delay interval should be reported
3. spectral power in the delay period should be analyzed

Exclusion criteria:

1. connectivity analysis
2. machine learning
3. the delay period overlapped with motor response (virtually all n-back studies)

The full table with 86 records is presented in Appendix 1 (Table A1). The flow chart with stages of the selection process is depicted in Figure 4.

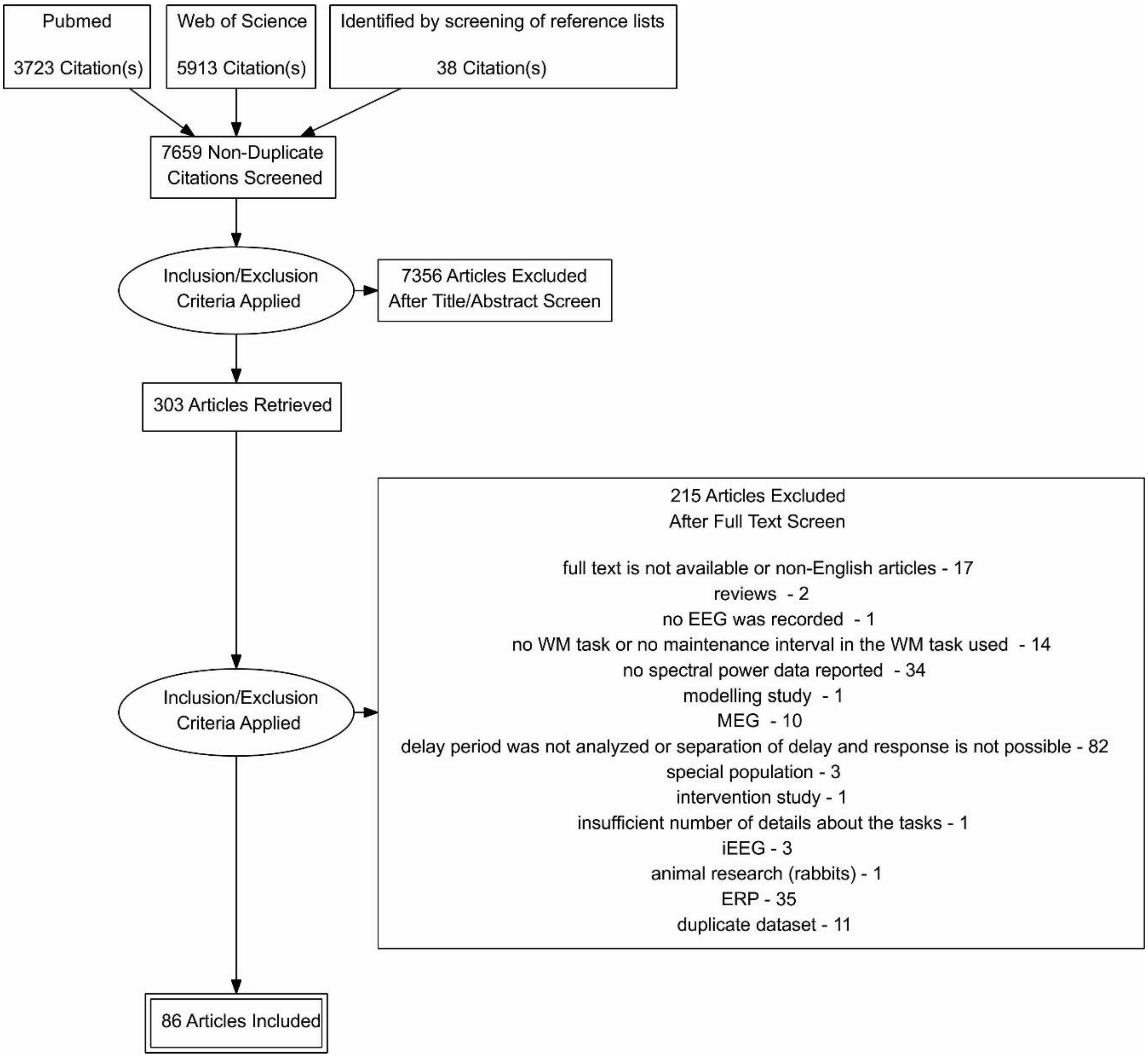

Figure 4 –Flow chart of the systematic review

1.2.2.4 General results

While being a cross-modal construct, WM can depend on stimulus modality (Daniel, Katz, & Robinson, 2016; Postle, 2006). Baddeley & Hitch’s model of WM overtly dissociates verbal and visual-spatial subprocesses. Some findings obtained in visual-spatial WM tasks may not generalize to verbal working memory. Verbal and visual-spatial subprocesses and associated with them phonological loop and visuospatial sketchpad have profound differences. A non-exhaustive list of the differences may include speed of memory decay, spatial and temporal distribution of associated neural activity, and encoding and consolidation time (Oberauer et al., 2018). A somewhat exclusive place of verbal WM is noticed in the last collaborative expert report summarizing research findings in WM research (Oberauer et al., 2018). Therefore, I shall focus the review on verbal WM as the most relevant to the current work (see Table A2 for a summary of the results).

Patterns of oscillatory activity obtained from EEG, MEG and iEEG data can be similar. However, a number of differences exist (Leijten, Huiskamp, Hilgersom, & van Huffelen, 2003; Malmivuo, 2012; Sharon, Hämäläinen, Tootell, Halgren, & Belliveau, 2007; Stefan et al., 1994). Not only physical properties of the signal are different but there is another complication making iEEG literature less generalizable. Human iEEG is most frequently recorded in epilepsy patients. The patients regularly take pain killers while recovering from the electrodes implantation, they also stop taking antiepileptic drugs to provoke seizures. Mild cognitive impairment that may take place in this population requires the cognitive tasks to be modified accordingly. Directly comparable research was the main target of the literature review. Nevertheless, for the sake of completeness, the results of EEG verbal WM studies will be complemented by MEG and iEEG results when appropriate. MEG and iEEG verbal WM studies were identified using similar procedure to the one used for the EEG systematic search of the literature.

Out of the 86 selected studies, the number of purely verbal WM studies was 29. In 2 studies verbal and visual tasks were used, 44 studies used visual tasks only, 1 study used a combination of visual and kinaesthetic stimuli, 2 studies compared visual, tactile and auditory stimuli, 4 studies used non-verbal auditory stimuli and 4 studies used tactile stimuli.

In verbal WM studies the task was presented auditorily in 4 of the 31 studies. In the other studies the task was presented visually. In 71% (22/31) studies the authors used the classic version of the Sternberg task. In 3 studies DMTS paradigm was used. In 3 other studies variations of more typical for behavioral studies simple/complex span paradigms with free recall were used. In one study one digit was an object of serial transformations (mental arithmetic), but the probe was a single item with yes/no response like in the classic Sternberg task. In one study the participants had to memorize sequentially presented letters and reproduce the sequence in the correct order at the end of the trial (serial recall). Finally, in one study a letter-digit combination was used as the probe, similarly to the task used in the current study (see Methods). Typically, letters (16/31), words (6/31), or digits (6/31) were used in verbal WM tasks. In two studies a combination of letters and digits and in the other study phrases describing chemistry concepts were used.

In the following sections I shall give a deeper overview of the four central questions of the review: how (1) WM load, (2) engagement of different WM components, (3) duration of the delay period and (4) individual differences affect neural oscillations in WM.

1.2.2.5 Load effects

41 of the 86 studies (48%) varied set-size and consequently WM load. The rest (45 studies) only compared the activity in the delay period with a baseline interval, or presented spectral power data without baseline correction. The proportion of the verbal WM studies exploring more than one level of difficulty (68%, 21/31) was larger in comparison with the other domains (36%, 20/55) ($\chi^2 = 7.8$, $p = 0.005$). Verbal experiments used single item to encode without additional levels of load only in one study (3%, 1/31). The proportion is significantly smaller than in the other domains (32%, 18/55) ($\chi^2 = 10.03$, $p = 0.002$). Figure 5 depicts the distribution of the levels of load in the WM domains. As can be seen in the figure, to vary the load starting from one item is quite typical in visual (23%, 22/94) but significantly less common in verbal (4%, 3/70) domain WM research ($\chi^2 = 11.35$, $p < 0.001$).

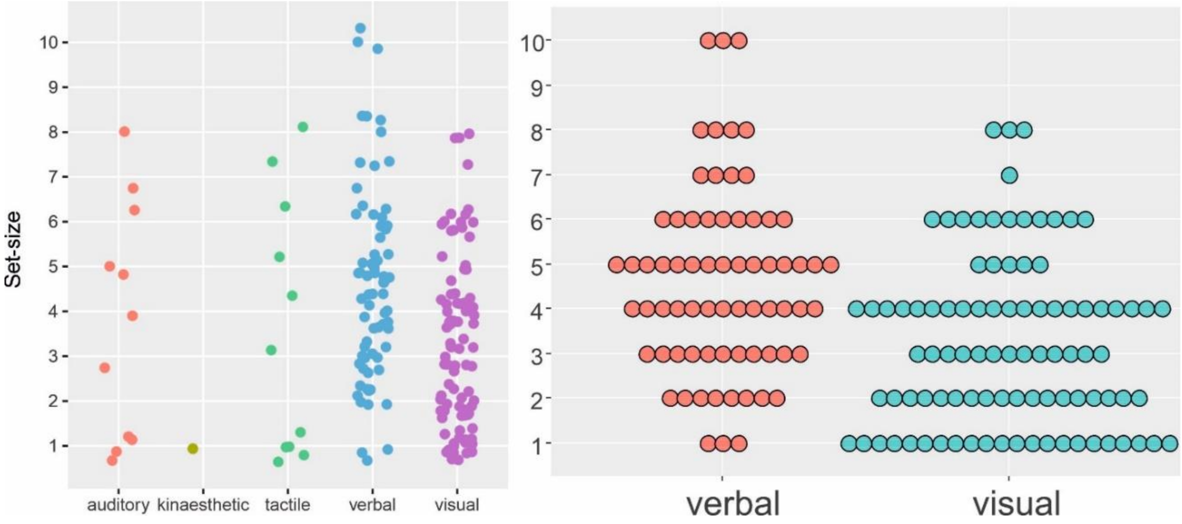

Figure 5 – Distribution of set-sizes by WM modality. Each dot represents one level of load in a study. Note that there are much more dots than studies because more than one modality could be used in a study as well as several levels of load.

The first question I aimed to answer with the review was how changes in WM load affect oscillatory brain activity during the delay period. In order to achieve that, I extracted data on absolute or relative spectral power in theta, alpha, beta, and gamma frequency bands. I included all of the 31 verbal WM studies and a representative sample of studies in other domains and methods (i.e., MEG and iEEG). WM load in the context of the review is defined as either comparison of several levels of load (e.g. 2 vs 4 items in WM) or comparison of any load with the baseline.

In 23 of 31 studies ***theta*** rhythm was featured in the results or depicted in figures. Theta has never been reported to decrease in verbal working memory tasks with an exception of one study (Harmony et al., 1996). The study reported a decrease of theta compared with the baseline, but only in a low load condition (memorizing 3 digits). All the other studies reported an increase of theta activity during delay. Another common finding frequently reported in the literature is an incremental increase of theta activity with load. The review identified 16 studies using the tasks with more than one level of WM load. The effect of step-wise increase of theta was found in 12 out of the 16 studies (see Table A2). In addition to the above mentioned study of Harmony et al. (1996), in one study the step-wise increase of theta activity was observed only in the high performance group (Pavlov & Kotchoubey, 2017). No observable and/or statistically significant load-dependent increase was found in two studies (Kwon et al., 2015; Schack & Klimesch, 2002). As we can see, EEG verbal WM research strongly supports the hypothesis of involvement of theta oscillation in WM delay processes.

The picture is less clear when iEEG and MEG data are taken into account. A number of methodological differences complicates a comparison between EEG findings and those obtained by other electrophysiological techniques. For example, one iEEG study, frequently cited in the context of WM load, used an unconventional frequency band (5-13 Hz) that does not allow to differentiate alpha and theta load dependent effects (Meltzer et al., 2008). Another iEEG study showed an increase of theta in the task (Raghavachari et al., 2001), but no incremental load dependent increase was observed. There is only one non-EEG study where incremental load dependent theta increase was demonstrated (Jensen & Tesche, 2002). Another MEG study found an FMT increase from 2- to 5-letters conditions but saturation in the 8-letters condition (Brookes et al., 2011). Moreover, three other studies did not report a continuous WM load-related increase of theta during delay period (Kustermann, Popov, Miller, & Rockstroh, 2018; Kustermann, Rockstroh, Miller, & Popov, 2018; Stephane et al., 2010). Only a short-lived transient increase but no continuous theta synchronization during delay period was found in the study by Proskovec, Heinrichs-Graham, et al. (2019). Similarly, another study conducted by the same group reported no theta change neither during encoding nor during delay period (Heinrichs-Graham & Wilson, 2015).

Heinrichs-Graham & Wilson (2015) noticed the discrepancy between their findings and the results of previous MEG studies. The authors explained the inconsistency by the difference between the simultaneous presentation of stimuli in their study and the successive presentation in other MEG studies where the effect was found (Brookes et al., 2011; Jensen & Tesche, 2002). However, the hypothesis is not supported by the data obtained in EEG verbal WM studies. The increase of theta with load was reproducible in both simultaneous (12 studies) and successive (11 studies) varieties of the Sternberg paradigm. This result highlights the difference between EEG and MEG in methodology and probably underlying biophysical mechanisms. At least in some cases results obtained by MEG and EEG should be interpreted interchangeably with caution.

In the classic Sternberg task only one item is probed. It means that maintaining the order of the presented items is irrelevant to the task. Hsieh et al. (2011) argued that theta is important to the maintenance of temporal order and less relevant in the tasks when only content information is stored in WM. A piece of evidence is provided by a MEG study that compared two conditions: (1) memorizing only content and (2) memorizing the content as well as location of the presented stimuli (Poch et al., 2010). In this study information about the order can be seen as the spatial dimension added to the verbal content. The authors found a stronger theta increase in the verbal-spatial condition in comparison with the verbal condition. However, the source of the theta was not attributable to medial frontal cortex or the ACC which are commonly found sources of FMT. It appears to be difficult to design a task which could provide sufficient evidence for or against this hypothesis in verbal domain. Moreover, even presented simultaneously verbal content is rehearsed in a sequence. It can be less of a problem for the visual WM domain. Moreover, in a visual Sternberg paradigm using unpronounceable shapes, theta effects were still observable (Maurer et al., 2015). Given the obvious limitation of verbal WM studies in the context of this hypothesis it can be beneficial to broaden the scope of this part of the review to the visual WM studies.

As will be reviewed in full in Section 1.2.2.7, many visual WM studies suffer from short delay intervals. Short delays may prevent a meaningful analysis of sustained oscillatory brain activity. I included in this analysis only WM studies with the delay period equal or longer than 1.5 s. This inclusion criterion will guarantee that the sustained theta activation is not contaminated by event-related response. The identical number of visual (30/49) and verbal (30/31) WM studies were included into the analysis. In this subsample 22/30 verbal and 15/30 visual WM studies featured theta in the results.

Verbal WM studies reported increase in theta significantly more frequently than visual ones (21/22 and 9/15 respectively, $\chi^2 = 7.3$, $p = 0.007$). Nevertheless, Khader et al. (2010) used both modalities and found no significant differences in theta expression. Similarly, Kawasaki et al. (2010) used two tasks with manipulations involving either auditorily presented verbal or spatial-visual information. Theta enhancement was observed in both tasks.

Among the 15 visual WM studies featuring theta effects, only 9 studies reported an increase in theta activity during delay. Three other studies found a decrease of theta and 3 studies reported null effects. Similarly to the verbal WM study by Harmony et al. (1996), two studies reported a decrease of theta in the conditions with very low WM load. For example, Babiloni et al. (2004) used a task where only the decision of which button to press had to be maintained, not the sensory information. Another study used a one item WM paradigm (Bastiaansen, Posthuma, Groot, & de Geus, 2002). In the last study the complexity of the task varied in an adequate range but nevertheless a significant decrease of theta was observed (Boonstra, Powell, Mehrkanoon, & Breakspear, 2013). However, data shown in the bottom panel of the first figure in Boonstra et al. (2013) (see my Figure 6 below) challenge the conclusion of theta suppression during delay. One can notice that 4-8 Hz frequency band designated by the authors as theta largely overlaps with alpha and shares its behavior. Taking into account this observation, sustained theta activity in this work was in fact absent.

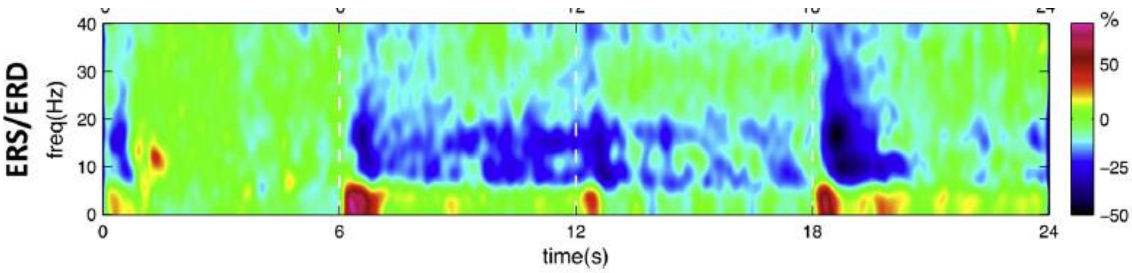

Figure 6 – Time-frequency representation of EEG spectral power during task performance. Maintenance interval is from 12 to 18 s. The figure is taken from Boonstra et al. (2013) with permission from Elsevier.

Boonstra et al. (2013) and the other three visual studies reporting null findings employed DMTS paradigms. Temporal order information is relevant in the Sternberg task but redundant in the DMTS type of task. Theta oscillations were hypothesized to play a significant role in maintenance of temporal relationship between the items in WM (Hsieh et al., 2011). This idea was supported by another study conducted by the same group (Roberts, Hsieh, & Ranganath, 2013). In this study the participants required to remember either location of 4 presented sequentially abstract images or temporal order of the images. Theta power was found to be higher in the order condition. Hsieh & Ranganath (2014) suggested that the function of theta enhancement with increasing demand on WM is the maintenance of more and more complex relationships between items in WM.

This hypothesis can be tested in the verbal WM domain in three ways. First, by comparison of single item WM load when no temporal relationship between items exists with higher load conditions. Onton et al. (2005) demonstrated the expected pattern of load-dependent increase of theta power (see Figure 7). Unfortunately, the delay period after the presentation of the items was too short to make a reliable conclusion. Out of 37 verbal and visual WM available studies, this is the only one where this kind of comparison could be made. Second, the explicit task requirement to memorize order and content in one condition and to memorize only content in another one could shed some light on the matter. For example, a comparison of the classic Sternberg paradigm with a single item probe and modified Sternberg similar to the one used in my dissertation with a requirement to remember both content and order would provide such evidence. To date there are no such studies. Third, more studies manipulating WM load in a wide range can provide additional evidence in support for the hypothesis.

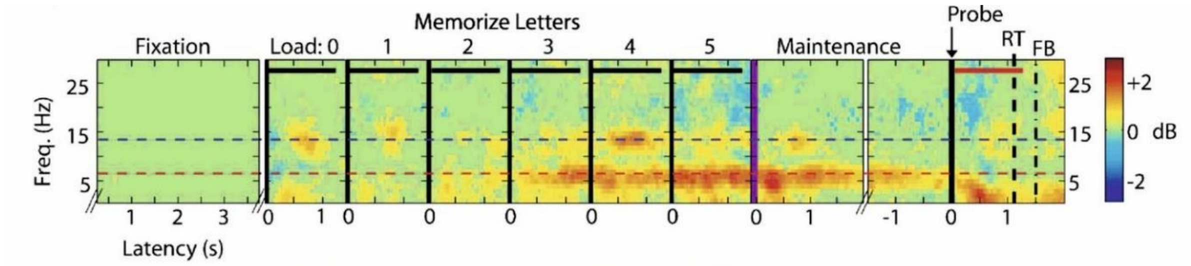

Figure 7 – Development of FMT enhancement with increasing load from 0 to 5 items in a verbal WM task. Black horizontal bars represent the encoding period (the figure is adapted from Onton et al. (2005) with permission from Elsevier)

In 25 out of 31 studies ***alpha*** rhythm was featured in the results or depicted in figures. Seventeen studies varied WM load in two or more levels. A change in alpha activity as a function of increasing load was observed in 12 of them. In two cases no incremental alpha increase/decrease with load was observed (Harmony et al., 1996; Kwon et al., 2015). There was a saturation effect in two studies (Bashivan et al., 2014; Xie et al., 2016, see below). In another study the load effect was neither statistically tested nor presented in a graphical form (Klimesch, Schimke, & Pfurtscheller, 1993). These results generally replicate the findings in theta frequency band – most studies report incremental load effects in alpha oscillations.

As compared with theta activity, there is more discrepancy concerning the direction of the effects. A clear task related increase of alpha activity was observed in 12/25 studies. In 7 studies there was a decrease of alpha during delay period. In the other 6 studies the results were more complex. In two studies alpha increased in the 4-items condition as compared with the 2-items condition, but no further increase in the 6- and 8-items conditions was observed (Bashivan et al., 2014; Xie et al., 2016). In another study Michels et al. (2008) distinguished two groups of subjects (N=9 in each group): a group where alpha increased with WM load and another group where alpha decreased. Interestingly, but not surprisingly, in two studies conducted by the same group on the same topic no individual differences in alpha reactivity were reported anymore (Kottlow et al., 2015; Michels et al., 2010). One study reported an increase of alpha in a right occipital channel but a decrease in a midline parietal channel (Kottlow et al., 2015). Similarly, in another study the alpha activity increased with load in right posterior channels but decreased in all other channels (Pavlov & Kotchoubey, 2017). Finally, Okuhata et al. (2013) found that alpha reactivity depended on the type of stimulus presentation.

There are two ways of presenting information in verbal WM tasks: simultaneously or successively. Okuhata et al. (2013) directly compared the two types of presentation. They reported a load-dependent increase of alpha in the successive presentation condition, but a decrease in the simultaneous presentation condition. In line with Okuhata et al. (2013), another group of authors also suggested that alpha activity mainly occurs in the tasks requiring maintenance of simultaneously presented information (Hsieh et al., 2011). Checking the evidence for this hypothesis in the verbal WM domain, I found that almost a half (15/31) of the reviewed studies used successive presentation (including all 4 auditory WM studies). Simultaneous presentation was also used in 15 of the 31 studies. The above-mentioned study of Okuhata et al. (2013) compared both presentation types. Using only 24 studies with unambiguous findings, no significant prevalence of the direction of alpha effects was found in the comparison between simultaneous (7/11 showed an increase) and successive (9/12 showed an increase) presentation ($\chi^2 = 0.35$, $p = 0.55$).

Verbal WM research employing other electrophysiological techniques consistently reports alpha enhancement during delay. The alpha increase was found in 6 MEG studies (Bonnefond & Jensen, 2012; Heinrichs-Graham & Wilson, 2015; Kustermann, Rockstroh, et al., 2018; Leiberg et al., 2006; Proskovec, Heinrichs-Graham, et al., 2019; Wianda & Ross, 2019). The parametric load-dependent alpha increase was found in 3 of them (Kustermann, Rockstroh, et al., 2018; Leiberg et al., 2006; Proskovec, Heinrichs-Graham, et al., 2019). In one MEG study alpha activity decreased during delay period (Stephane et al., 2010). In an iEEG study the direction of changes in a combined theta/alpha frequency band (5-13 Hz) varied depending on the location of the electrode (Meltzer et al., 2008). A load-dependent decrease was observed in the right occipital cortex, whereas an increase was found in the left temporal area. The choice of frequency band complicates the interpretation of these results.

In a narrative review van Ede (2018) selectively compared a few studies using either visual or verbal WM tasks. van Ede suggested that the sign of alpha modulation depends on the nature of memoranda: visual content maintenance results in alpha suppression, and verbal content maintenance leads to alpha increase. In order to test this hypothesis, I included to this analysis only the studies with the duration of delay period equal or longer than 1.5 s. This inclusion criterion allows to take into account a bias towards shorter delay periods in visual WM studies that complicates the issue with event-related potentials mentioned above. Most verbal WM studies (65%, 13/20) reported alpha increase, but 67% (16/24) visual WM studies reported the increase as well ($\chi^2 = 0.01$, $p = 0.9$). This analysis clearly shows a weakness of van Ede's hypothesis. The modality of WM does not warrant a sufficient explanation of the discrepancy in the alpha effects. No other specific detail of the experimental design used in the reviewed studies can point out to other unambiguous explanation of the difference in the direction of the alpha effects.

Only 13 out of 31 studies featured ***beta*** frequency band (13-30 Hz) in the results or depicted in figures. Null findings were reported in 3/13 cases. In 6/13 cases beta power was reported to be suppressed with WM load. In the other 4 cases beta power increased during the delay period.

Frequencies and spatial distributions of the beta effects varied substantially. Lower beta or beta1 (typically 13-20 Hz) was analyzed in 6 cases, higher beta or beta2 (20-30 Hz) was analyzed in 2 cases, and in 5 cases the whole frequency band was inspected. In 5 studies beta covered posterior channels, in 4 studies beta was located at frontal sites, and in two studies both frontal and posterior sites were included into analysis. No particular pattern of beta activation/suppression in these studies was related to the spatial distribution. In one study higher beta increased at frontal sites in the high performance group but increased at posterior sites in the low performance group (Pavlov & Kotchoubey, 2017). Another study presented verbal stimuli auditorily and found an increase of lower beta in the T3 and T4 channels only (Stokic, Milovanovic, Ljubisavljevic, Nenadovic, & Cukic, 2015). These channels are frequently heavily contaminated by muscle artifacts.

In verbal WM MEG studies beta effects are widely spatially distributed as well. Thus, Brookes et al. (2011) used a Sternberg task and found a load-dependent decrease of beta over the frontal medial lobe. In support of Stokic et al.'s (2015) findings an auditory verbal WM MEG study found an increase of lower beta over temporal areas as well (Leiberg et al., 2006). In a complex verbal-spatial task beta increased at parietal and frontal sources (Poch et al., 2010). Widely distributed beta activity showed an effect of suppression during delay period in another study (Stephane et al., 2010). Continuous beta suppression over the left central area was shown by Wianda & Ross

(2019). In turn, beta in occipital sensors behaved similarly to alpha and increased in this study. No iEEG studies reported effects in the beta range.

Beta oscillations in verbal WM research are much less studied than alpha and theta. The review has shown a wide diversity of the effects in the beta frequency band. An assumption that there is probably more than one beta rhythm may contribute to the explanation of the discrepancy in the effects. These beta rhythms may occupy different frequencies, have different temporal and spatial distribution and, therefore, different functional meanings. At the moment the role of beta oscillations in verbal WM remains unclear.

EEG **gamma** activity in verbal WM tasks is even less well studied. Gamma activity results were featured in 4/31 studies. In 3 of the 4 studies null findings were reported and in one study gamma demonstrated a decrease in comparison with the baseline. Generally, the EEG signal in the gamma range is much noisier than in lower frequencies, which may explain less attention to gamma oscillations in EEG and verbal WM tasks.

MEG and iEEG studies show more promising data. One MEG study demonstrated a decrease of beta/low gamma oscillatory power with increasing WM load (Brookes et al., 2011). Gamma decrease with load was also shown in another study (Stephane et al., 2010). Gamma increase in more challenging conditions was demonstrated in two other verbal WM MEG studies (Kustermann, Rockstroh, et al., 2018; Poch et al., 2010). The increase of gamma power with load was found in 6 of 9 available iEEG studies (Bahramisharif, Jensen, Jacobs, & Lisman, 2018; Gehrig et al., 2019; Howard et al., 2003; Kambara et al., 2017; Mainy et al., 2007; Meltzer et al., 2008). Even this high percentage (67%) can be an underestimation. Of the three studies with "negative" findings, two studies recorded iEEG from hippocampus (Boran et al., 2019; Leszczyński, Fell, & Axmacher, 2015), which cannot be directly compared with the cortical iEEG. Finally, the last study (Raghavachari et al., 2001) briefly mentioned that gamma activity was affected by load but the results are reported elsewhere. Unfortunately, I was unable to identify the referenced study.

The number of EEG verbal WM studies featuring gamma is small. The results are rather contradicting and inconsistent with other electrophysiological modalities. Furthermore, the disproportionally large share of iEEG studies reporting gamma effects suggests that the superficial EEG may not be the best tool to study gamma oscillations.

1.2.2.6 Components of WM

The second key question of the systematic review is how different components of WM are represented in EEG oscillations. To answer this question, I looked at the studies comparing WM tasks including both maintenance and manipulations (i.e., genuine WM tasks) and tasks with maintenance of information only (i.e., STM tasks). In total, 10% (9/86) of all the studies used genuine WM tasks. Five of them used verbal content and four were visual WM studies.

Berger et al. (2014) compared WM delay EEG in manipulation and retention tasks. Two types of manipulations were used: mental sequencing 4-letters strings into alphabetical order or backwards reordering of the letters. The authors report an increase of frontal midline theta in both manipulation tasks in comparison with the simple retention condition. Moreover, the alphabetical task led to a larger increase of theta than backwards reordering. Alpha power decreased in both manipulation conditions but was indifferent to the type of manipulation. Finally, lower beta (13-20 Hz) in posterior channels showed a decrease in both manipulation conditions with a stronger decrease in the alphabetical condition. Griesmayr et al. (2010) used simple retention and the alphabetical type of manipulation with 3 letters strings and also found an increase of theta power in the manipulation condition. In our previous study we found a similar relationship between FMT and the manipulation task with alphabetical reordering (Pavlov & Kotchoubey, 2017). Another finding was a significant suppression of alpha and lower beta activity in the manipulation as compared with the simple retention task.

Kawasaki et al. (2010) used tasks involving different types of manipulation. In one of the tasks the participants were required to perform mental addition with auditorily presented digits. The second task was to mentally move a dot in 5x5 grid updating its position after corresponding commands. The aim of the study was to compare manipulations in visual and auditory WM domains. This fact complicates interpretation of the results in the context of the other studies. However, verbal manipulations were accompanied by an increase of FMT power and the left parietal and frontal alpha activity. Another study compared manipulation (update of content with a new item) and simple retention conditions (Itthipuripat, Wessel, & Aron, 2013). Confirming the findings of the above referenced studies, extended theta synchronization characterized the manipulation task more than the task to maintain the information without manipulations.

Neither MEG nor iEEG studies (including the visual ones) compared manipulation and retention conditions.

All available electrophysiological data, including 4 visual EEG WM studies (Eschmann, Bader, & Mecklinger, 2018; Kawasaki et al., 2010; Kawasaki & Watanabe, 2007; Sauseng, Klimesch, Doppelmayr, et al., 2005) converge on the importance of FMT in manipulation of information in WM. The difference between tasks with manipulations and a simple retention task is in the level of involvement of executive components of WM. Therefore, FMT is thought to reflect engagement of executive components of WM (Sauseng, Griesmayr, Freunberger, & Klimesch, 2010). The role of alpha and beta activity is less clear.

The question of spatial properties of WM delay activity has a long history stemming from animal research and human neuroimaging studies. Early works in monkeys proposed the model of WM postulating that information during delay period is stored in the frontal cortex (Fuster & Alexander, 1971; Goldman-Rakic, 1995; Jacobsen, 1935). However, human fMRI (Curtis & D'Esposito, 2003; D'Esposito et al., 1998; Narayanan et al., 2005; Ranganath, DeGutis, & D'Esposito, 2004) and non-human primate (Pasternak & Greenlee, 2005) studies consistently reported a parallel activation of frontal and parietal areas during the delay period. Recent research employing multi-voxel pattern analysis suggests the engagement of different brain regions depending on the modality (Christophel, Klink, Spitzer, Roelfsema, & Haynes, 2017) (see Figure 8). Information about speed and direction (Riggall & Postle, 2012), contrast (Xing, Ledgeway, McGraw, & Schluppeck, 2013), orientation (Albers, Kok, Toni, Dijkerman, & de Lange, 2013), color (Serences, Ester, Vogel, & Awh, 2009) of visual stimuli can be manifested in BOLD signal sourced from the visual cortex. Similarly, the precentral and intra-parietal sulcus found to encode to WM spatial information (Jerde, Merriam, Riggall, Hedges, & Curtis, 2012; Sprague, Ester, & Serences, 2014). Auditory tone features are stored by auditory cortex (Kumar et al., 2016), and tactile information can be decoded from parietal and premotor cortex activation (Schmidt & Blankenburg, 2018; Schmidt, Wu, & Blankenburg, 2017).

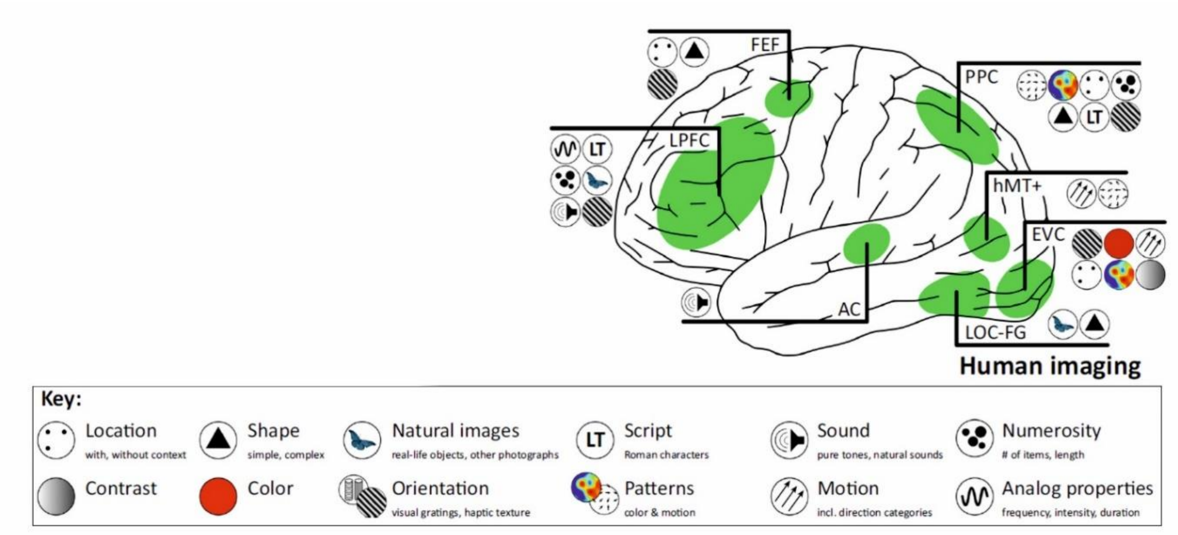

Figure 8 – Brain areas typically activated in WM tasks. Notes: FEF, frontal eye fields; AC, auditory cortex; EVC, early visual cortex; hMT+, middle temporal/medial superior temporal; LOC, lateral occipital complex; LPFC, lateral prefrontal cortex; PPC, posterior parietal cortex. Figure modified from Christophel et al. (2017) with permission from Elsevier.

In contrast to electrophysiological studies, components of WM are of sufficient interest in neuroimaging community. Thus, one the most cited (3290 citations as for 19.07.2019) articles in the neuroscience of WM (Smith & Jonides, 1999) is specifically dedicated to the analysis of brain correlates of temporary storage and central executive components of WM. A comparison of fMRI-BOLD responses in manipulation and retention tasks indicates the role of frontal lobes in WM. In an early meta-analysis Wager & Smith (2003) found the superior frontal sulcus and the DLPFC to be involved in manipulation of information in WM. A more recent meta-analysis of 36 studies dedicated to the executive components of WM pointed in the same direction (Nee et al., 2013). In verbal WM tasks the most prominent peaks of activation selectively associated with executive components of WM are localized in the superior frontal sulcus and mid-lateral frontal cortex. In addition, patients with local lesions in the DLPFC in comparison with non-DLPFC patients exhibit reduced performance in manipulation tasks without a deficit in retention tasks (Barbey, Koenigs, & Grafman, 2013).

To summarize, according to the current view, sensory information is maintained in WM by the same cortical areas that are responsible for information encoding. The role of the prefrontal cortex in this model is to focus attention on the relevant sensory representations, to suppress the irrelevant sensory input and to manipulate the information.

Sufficient interest in neural correlates of WM components WM is not spreading far beyond the fMRI community. As was shown in the systematic review above, only a small portion of EEG works actually studied WM and not only STM. The data provided by fMRI help us to understand spatial properties of the neural networks underlying maintenance and manipulation of information in WM. How the information flows are coordinated on a finer time scale is not so easy to understand using fMRI. More EEG research is needed to elucidate oscillatory correlates of functional components of WM.

1.2.2.7 Duration of delay period

Delay periods in behavioral research vary in a wide range (Berman, Jonides, & Lewis, 2009; Lewandowsky, Oberauer, & Brown, 2009; Oberauer et al., 2018), from less than a second to tens of seconds. EEG can potentially track brain activity on the time scale of single neuron activation. It seems beneficial to take the full advantage of this feature and expand our knowledge about WM delay activity in different time scales. However, not many electrophysiological studies have taken this opportunity. The majority used very short delay periods diminishing the additional value of electrophysiological measures. Furthermore, typical for EEG research short delay periods may complicate interpretation of the findings in the context of numerous behavioral studies.

The most commonly employed WM paradigm nowadays is the lateralized change detection task. CDA is used as an index of STM in this paradigm. As shown by Fukuda et al. (2015) CDA lasts for no longer than 1 s. CDA is reminiscent of iconic memory, which also lasts for a period of about a second (Sperling, 1960). Nevertheless, the experiments with masking, which is suggested to clear the sensory register, provide evidence against the direct relationship between iconic memory and CDA (Vogel, Woodman, & Luck, 2006). Interestingly, neuropsychological studies with medial temporal lobe patients demonstrated the lack of deficits in the WM tasks with very short delays (1 s) but clear impairment in the WM task with a longer (7 s) delay (Nichols, Kao, Verfaellie, & Gabrieli, 2006; Olson, 2006). How such a short-lived ERP phenomenon as CDA corresponds to WM is a matter for a separate investigation.

However, the same study by Fukuda et al. (2015) showed that memory related alpha desynchronization lasts for about 3.5 seconds and then disappears. Although behavioral research in healthy volunteers provides us with converging evidence of zero or small effect of the delay duration on WM performance, brain activity during the delay period is probably not constant.

In verbal studies, the duration of the delay period varied in a range of 0.5-60 s, in the other modalities from 0.5 to 7.5 s. Some studies used variable delay duration. In these cases, I took the longest intervals. To account for outliers, the median instead of the mean value was used as a central tendency measure. The median duration of the delay period across all 86 studies was 2.28 s. Duration of the delay in verbal modality was longer than in the other modalities (median 3 s vs 2 s, U = 590, p = 0.014).

A visual WM study used 6 sec long delay period and found a dissociation between its early and late parts (Ellmore, Ng, & Reichert, 2017). The early delay was characterized by a prevalence of alpha activity, but after about 4 s alpha completely disappeared, which characterized the onset of the late delay. To investigate the consistency of this effect I selected studies with delays equal to or longer than 4 s. In total, 16 such studies were identified (see Table A1). Ten of them were verbal studies. In 6/16 studies the authors employed versions of time-frequency analysis that make it possible to visually assess the presence of the effect.

In the Ellmore et al. study alpha showed a transient effect vanishing after 4 s of the delay. In line with Ellmore et al. findings, alpha was not continuous throughout the delay in another study (Bastiaansen et al., 2002). The alpha reached the peak at 2.5 seconds and then started slowly fading out. In Figure 9 taken from a EEG-fMRI verbal WM study we can observe the load dependent alpha increase effect (left panels) (Scheeringa et al., 2009). In the first time interval the amplitude of alpha was large, reached the peak at 1.5-2 s and then started declining reaching the baseline level at about 6 s. For comparison, theta effect was more stable (Figure 9 right panels) and did not change as a function of time. The dynamics of alpha activity was also noticeable in another verbal WM study (Klimesch, Doppelmayr, Schwaiger, Auinger, & Winkler, 1999). Occipital alpha was decreasing (below baseline level in the higher load condition) in the first 5 sec of delay and then demonstrated an increase. In another study alpha returned to baseline at about 3.5 s after a period of continuous suppression

(Fukuda et al., 2015). Though in the last study alpha was suppressed the whole time showing similar dynamics throughout the whole delay period (Boonstra et al., 2013).

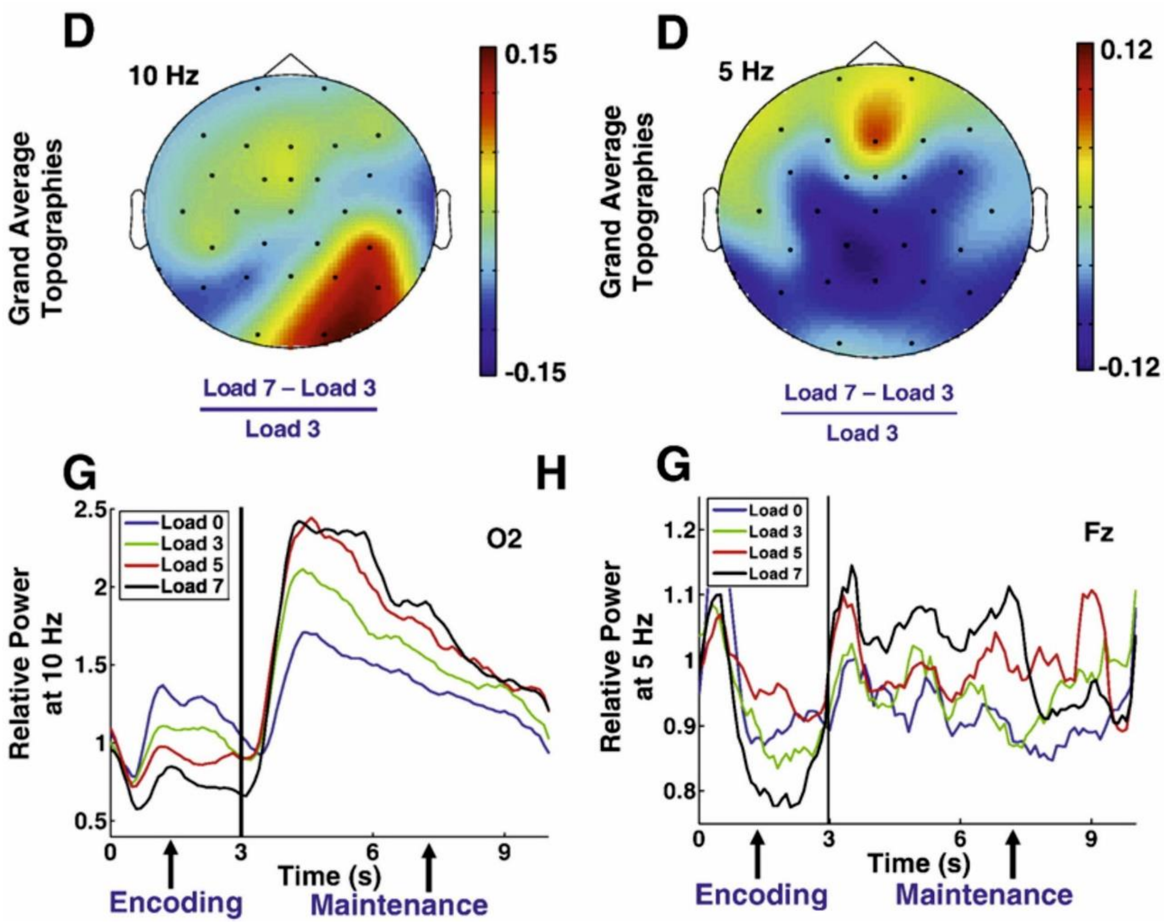

Figure 9 – Left panels: load effects on alpha activity. Right panels: load effects on theta activity. (adapted from Scheeringa et al. 2009 with permission from Elsevier)

Two MEG studies employing the classic Sternberg task showed alpha increase in the 3 sec delay period (Heinrichs-Graham & Wilson, 2015; Proskovec, Heinrichs-Graham, et al., 2019). Even though both studies used an identical task, the results were different (see Figure 10). In Proskovec, Heinrichs-Graham, et al. (2019) the alpha peaked at about one second, then started to decrease and at about 2.3 seconds the effect was inverted (Figure 10 left panels). No alpha decay can be observed in the other study (Figure 10 right panel). The same pattern of no decay was replicated in 6 other studies conducted by the same group in different samples including children, adolescents, elderly and clinical populations (Embury et al., 2018, 2019; McDermott et al., 2016; Proskovec, Heinrichs-Graham, & Wilson, 2016; Wiesman et al., 2016; Wilson et al., 2017).

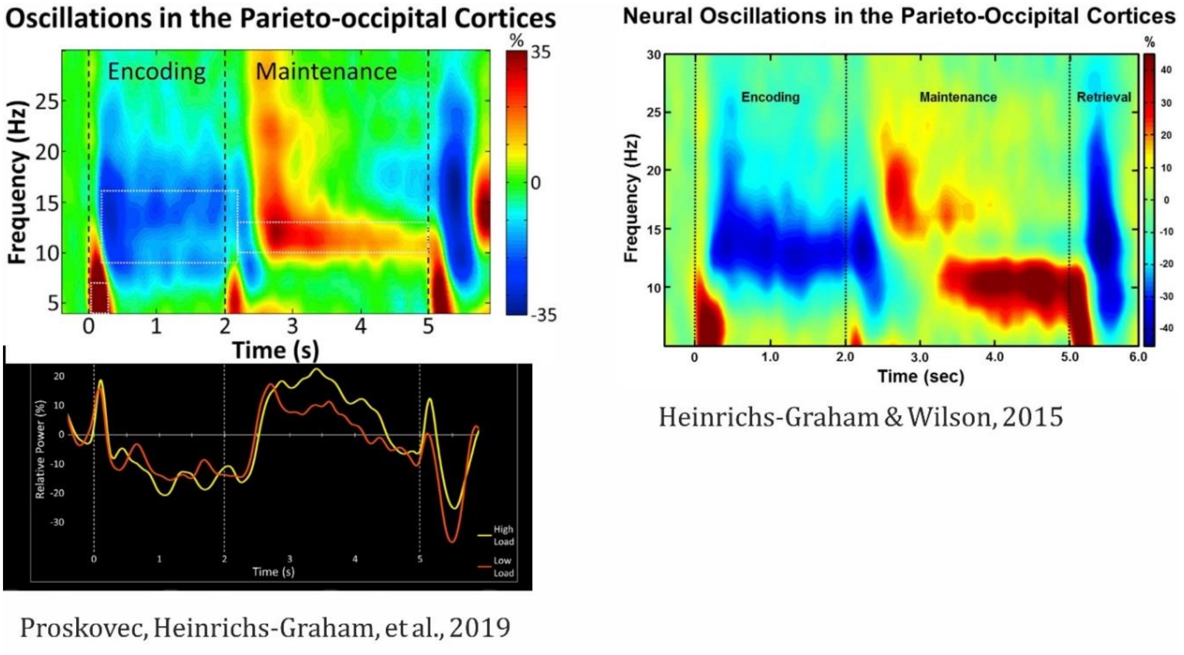

Figure 10 – Inconsistent alpha effects during delay in the same paradigm. Adapted from Heinrichs-Graham & Wilson (2015) and Heinrichs-Graham & Wilson 2015; Proskovec, Heinrichs-Graham, et al. (2019) with permission from Elsevier.

To summarize, there is no clear answer to the question of how stable the oscillatory activity is during WM delay. Maintenance of information in WM might be not as a unitary phenomenon as it is assumed by the studies using other neuroimaging techniques such as fMRI. In their recent article Baddeley & Hitch (2019) recognized this limitation of fMRI and appraised the use of EEG. The authors noted that the localization approach being the essence of fMRI findings has limited value for the multicomponent theories of WM. In their own theory WM hinges on fast interactions between subcomponents of WM that is impossible to see with a method having a time resolution in the order of seconds.

1.2.2.8 Individual differences in WM

The number of participants did not significantly differ between the studies carried out in verbal (mean ± SD = 20.51 ± 14.98) and other modalities (mean ± SD = 22.62 ± 23.27) (t(84) = 0.45, p = 0.65).

Individual differences were under consideration in 7 studies. Four of them used verbal WM tasks. To study individual differences, large samples are essential. It is particularly important when the whole sample of a study is subdivided into groups post hoc and between-subject statistical tests are used. In one study sample sizes of the low- and high-performance groups were 8 and 9 subjects respectively (Kwon et al., 2015). Any results derived from such a low powered study are meaningless and cannot be trusted. Another small sample study correlated alpha and beta power with behavioral performance (N=15) and found no significant relationship between the two (Bashivan et al., 2014). In non-verbal WM domains, conclusions are sometimes built on the comparison of groups with N=10 (Hsieh et al., 2011) and correlation with N=14 (Kawasaki & Yamaguchi, 2013). Not surprising that the hypothesis of Hsieh et al. (2011) concerning alpha directionality was disproved by overwhelming evidence (see Section 1.2.2.5). There was one non-verbal study with a sufficient sample size (Pahor & Jausovec, 2017). After initial screening of 125 volunteers, two groups of high- and low-performers were created with 30 individuals in each of them. The groups were determined by taking one standard deviation above and below the mean performance in the initial sample. Since, however, the authors used the change detection paradigm that implies a very short delay period (1 s), the findings cannot be extrapolated to the current work. Similarly, Fukuda et al. used the same task to test a correlation in a sample of 28 individuals.

As regards verbal WM studies, Maurer et al. (2015) found in a group with N=24 that the decrease of the accuracy with increasing task complexity correlated with theta activity (the steeper the decrement of the accuracy, the stronger the increase of theta power). In an adequately powered study Zakrzewska & Brzezicka (2014) looked at FMT in low (N=35) and high (N=34) WM performance individuals. The parametric increase of theta power with WM load was only present in the high-performance group. In the low-performance group, the increase of WM load did not affect theta activity. Moreover, the change in theta power from a low (2 letter) to high (5 letters) load correlated with the operation span score. In our previous study we identified a number of differences between low (N=33) and high (N=32) performance individuals (Pavlov & Kotchoubey, 2017). First of all, high performance individuals had stronger alpha activity. Like in the Zakrzewska & Brzezicka's (2014) work, FMT increased with load only in the high performance group. Finally, low beta (13-20 Hz) activity decreased in a manipulation task in comparison with a simple retention task but only in the high performance group.

A visual WM iEEG study (N=13) found that theta recorded over the DLPFC negatively correlated with load and positively with RT (Brzezicka et al., 2019). In other words, load-dependent theta decrease in the DLPFC related to better WM performance. I failed to identify any verbal WM studies employing iEEG or MEG that studied individual differences.

The ability to control attention and capacity of short-term storage may contribute to individual differences in WM in different scale (Kofler, Rapport, Bolden, Sarver, & Raiker, 2010; Unsworth & Spillers, 2010). Neural underpinnings of these contributions are unknown. By employment of tasks with manipulations in EEG research it is still possible to learn more about contribution of WM components to individual differences.

1.3 Objectives and Hypotheses

About 90% of EEG studies employed tasks which were only able to investigate the STM construct. Much less progress has been made to understand brain mechanisms supporting the essence of WM construct – the interplay between the retention and executive components of WM. Not enough progress has been made to understand the neural underpinnings of individual capacity limits in the last 25 years of extensive research of WM in psychophysiology. Therefore, I pursue two main goals in the current work: (1) to study oscillatory correlates of sensory storage and central executive components of WM and (2) to assess the contribution they make to individual differences in WM performance.

In order to reach these goals a large number of participants were tested in WM tasks of average to high complexity with and without manipulations. Increasing the complexity of the tasks allowed to increase the variance, to avoid ceiling effect in performance and to better distinguish between low and high performers. A task including mental manipulations allowed to assess the contribution of different WM components.

Based on the analysis of the literature, a number of predictions regarding neural activity during the delay period can be made. Most importantly:

1. Increased WM load and the necessity to suppress distractors in the manipulation task is hypothesized to lead to increased alpha activity.

2. The ability to suppress distractors can be a basis for individual differences; therefore, alpha is expected to differentiate individuals with different capacity limits.
3. As shown in the systematic review, load dependent enhancement of theta is a well-reproducible effect. Some previous studies related theta to the executive mechanisms of the brain and thus I expect FMT to increase with load and to be stronger in the task with manipulations than in the simple retention task.
4. Latent variable analyses of behavioral data showed a larger contribution of executive component of WM to individual differences. I expect to observe larger differences between participants in the manipulation condition than in the retention condition on the level of EEG data.
5. Based on multiple observations by Ruchkin et al. I expect to observe a negative SCP in fronto-central areas. The SCP is expected to become more negative with increasing load.
6. Retrieval P3b is expected to decrease with load and to be positively correlated with task performance.

The data were explored in three domains: behavior, time domain (event-related potentials) and time-frequency domain (changes in spectral power of different EEG oscillations). Event-related potentials with latencies shorter than 1 s will be referred to as ERPs, while long-latency slow potentials will be designated by the term slow cortical potentials (SCP). The results section of the manuscript consists of two main parts: description of general effects and individual differences. The reason for this separation is the difference in employed statistical approaches. Linear mixed-effects models were used to explore individual differences and a more familiar factorial analysis of variance (ANOVA) was used to test general effects. In order to explain the common sources of variance affecting WM performance in the current work, in the discussion I will return to the structure used in the systematic review.

METHODS

2.1 Participants

186 individuals participated initially in the study. Eight participants with overall performance below 60% were excluded. Furthermore, a subsequent analysis revealed 22 EEG records with an excessive amount of artefacts (less than 12 clean trials in any condition). Thus, 156 participants (82 females, mean age = 21.23, SD=3.22) were included to the final sample. The participants had normal or corrected-to-normal vision and self-reported no history of neurological or mental diseases. All the participants were Russian native speakers.

2.2 Stimuli

Sets of Russian alphabet letters written in capitals were used as stimuli. The letters had been selected randomly from the alphabet, had random order, and no repetitions in the sets. An analogue using Latin letters and English words is shown in Figure 11

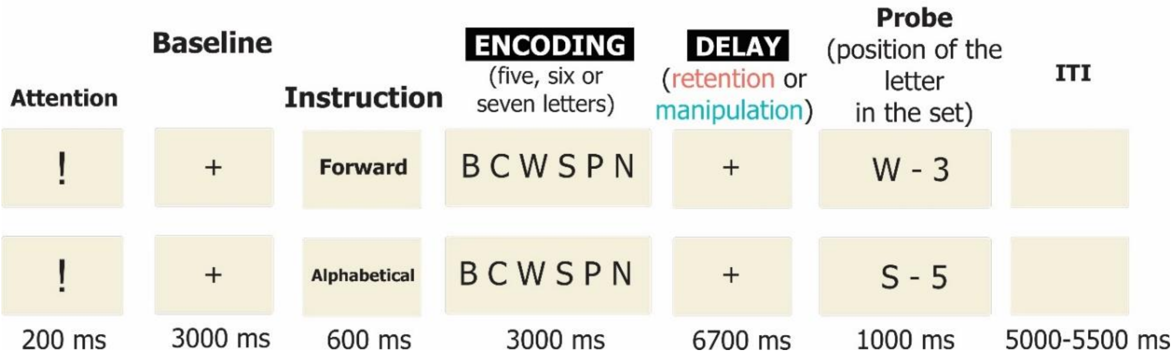

Figure 11 – The experimental paradigm

A trial always began with an exclamation mark presented for 200 ms, which was followed by a fixation cross for 3000 ms. Participants were instructed to fixate on the cross whenever it appeared. Next, the word “forward” or “alphabetical”, presented for 600 ms, instructed the participants whether they would have to maintain in memory the original set as it was presented (retention task) or, first, mentally reorganize the letters into the alphabetical order and then maintain the result in memory (manipulation task). After that, sets of 5, 6 or 7 letters were demonstrated for 3000 ms followed by a delay period where a fixation cross was demonstrated for 6700 ms. At the end of the delay period, a randomly chosen letter from the previously presented set appeared on the screen together with a digit that represented the serial number of this letter. The letter-digit probe was presented for 1000 ms. Depending on the task, the participants indicated whether the probe was on the corresponding position either in the original set (retention task), or in the set resulted from the alphabetical reordering (manipulation task). The participants were asked to press one of the computer mouse buttons (left or right) if the probe was correct and the other button otherwise. The two buttons were attributed to the correct and wrong probes in a counterbalanced order. The probe was correct in 50 % of the trials, and the order of correct and incorrect probes was randomized. The next trial started after a blank interval that varied between 5000 and 5500 ms.

The experiment entailed six different conditions: maintenance in memory of 5, 6 or 7 letters in the alphabetical (manipulation condition) or forward (retention condition) order. Each condition had 20 consecutive trials. These six blocks of 20 trials were presented in a random order. Two practice blocks with 3 and 6 trials respectively were given shortly before the main experiment.

During the experiment, the participants were seated in a comfortable armchair in front of a computer screen in a dark room. Stimuli were presented in white color on a black background in the center of the screen by using PsyTask software (Mitsar Ltd.). The distance to the screen was 1 m and the size of the letters was 1.2 × 1.2°.

2.3 EEG recording and analysis

The EEG was recorded from 19 electrodes arranged according to the 10-20 system using Mitsar-EEG-202 amplifier with averaged earlobes reference. Two additional electrodes were used for horizontal and vertical EOG. EEG data were acquired with 500 Hz sampling rate and 150 Hz low-pass filter.

The procedure of EEG artifacts suppression and removal was conducted in two steps. At the first step, in order to suppress ocular activity artifacts, the independent component analysis (ICA) was performed using AMICA algorithm (Palmer, Kreutz-Delgado, & Makeig, 2012). For ERP/SCP and time-frequency analyses I used different filter settings. Nevertheless, in order to improve the quality of independent components extraction, the ICA was run a single time with 1-45 band-pass filter (Winkler, Debener, Muller, & Tangermann, 2015). The generated IC weights matrix was applied to all the datasets and the same components were removed from each of them. Components clearly related to blinks and eye movements were identified and removed after visual exploration of the data. At the second step, epochs still containing artefacts were visually identified and discarded in all three analyses independently after the epochs extraction (see below for details).

EEGLAB toolbox (Delorme & Makeig, 2004) for Matlab was used for data preprocessing. ERPlab toolbox for Matlab was used for epochs extraction and rendering of topographical plots in SCP analysis (Lopez-Calderon & Luck, 2014). The time-frequency analysis was performed by means of the Fieldtrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011).

2.3.1 Event-related potentials

Before ERPs and SCP analyses each recording was filtered by applying 0.01 high-pass, 45 Hz low-pass and 50 Hz notch filters. Three events were used as triggers for the ERPs analysis: onsets of the encoding (presentation of the sets of letters), delay period (fixation cross) and retrieval (presentation of the probe).

The data were epoched in [-1200 1000 ms] intervals where 0 is the onset of the events. [-200 0] interval was used for baseline correction in the delay and retrieval conditions. Task instruction indicating the type of memorizing (forward or alphabetical) was presented in a close succession with the onset of encoding. For this reason and in order to have a more stable baseline, the baseline correction of the encoding condition was shifted to a [-800 -600 ms] time interval. ERPs were then averaged in 6 task-related conditions (memorizing 5, 6 or 7 letters sets in manipulation or retention conditions) and three time-related conditions (encoding, delay and retrieval).

Several time windows were defined based on the condition blind visual exploration of the grand average ERP curves in three midline channels (Fz, Cz, Pz) in three time-related conditions. The extracted time windows are marked in Figure 12. Encoding: P3a [180 300 ms], P3b [350 500 ms]; Delay: P2 [80 190 ms], P3a [200 300 ms], P3b [350 480 ms]; Retrieval: P3a [200 300 ms], P3b [360 600 ms]. Note that P3a was defined as the prominent positive peak between the typical P2 and the typical P3b; I do not claim that this P3a is identical to the P3a described in most normal cases (as reviewed, e.g., by Polich, 2007).

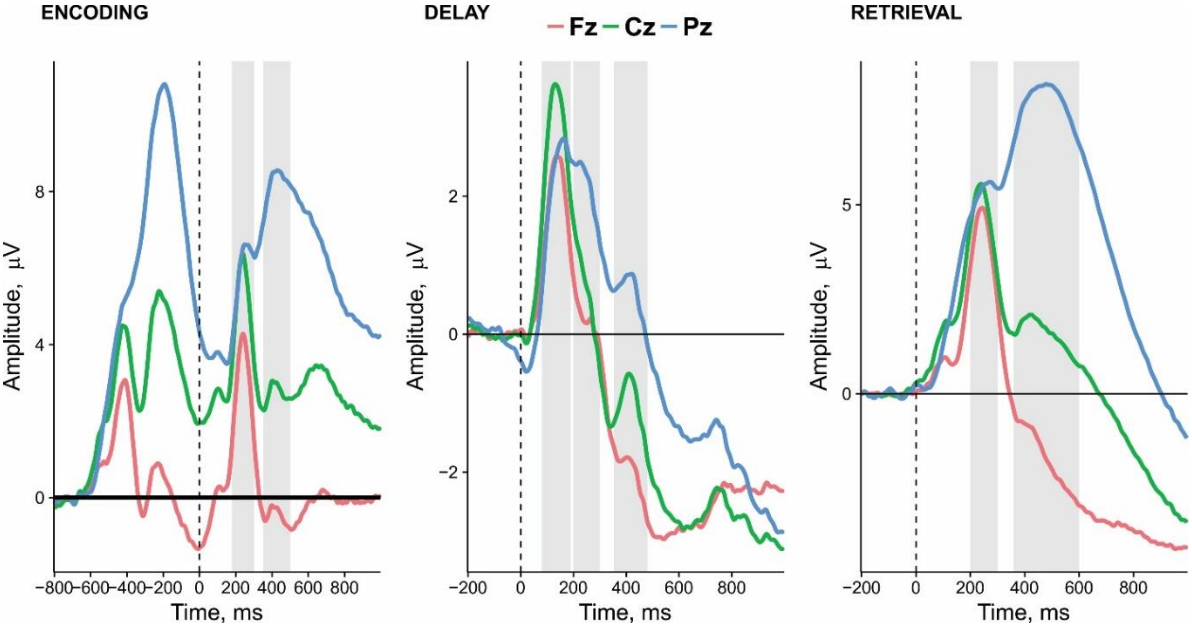

Figure 12 – Time windows for ERP analysis.

2.3.2 Slow cortical potentials

For SCP analysis epochs in [-14200 2200 ms] interval where 0 is the onset of the probe were created. The time interval between -11500 and -10500 ms corresponding to 1 s of the baseline time period (i.e. “Baseline” in Figure 11) was used for baseline correction.

SCP were averaged in 6 experimental conditions and in three time windows. The first window is the time interval corresponding to the presentation of the stimuli (2500 ms starting from 500 ms after the onset of the memory sets, see Figure 13). The first time interval will be referred to as Encoding. Then, the segment of 6000 ms corresponding to the delay period starting from -6000 ms to 0 ms where 0 is the onset of the probe was divided into two time intervals. The delay was also separated into two time intervals Delay1: the first 3000 ms of the delay and Delay2: the second 3000 ms of the delay.

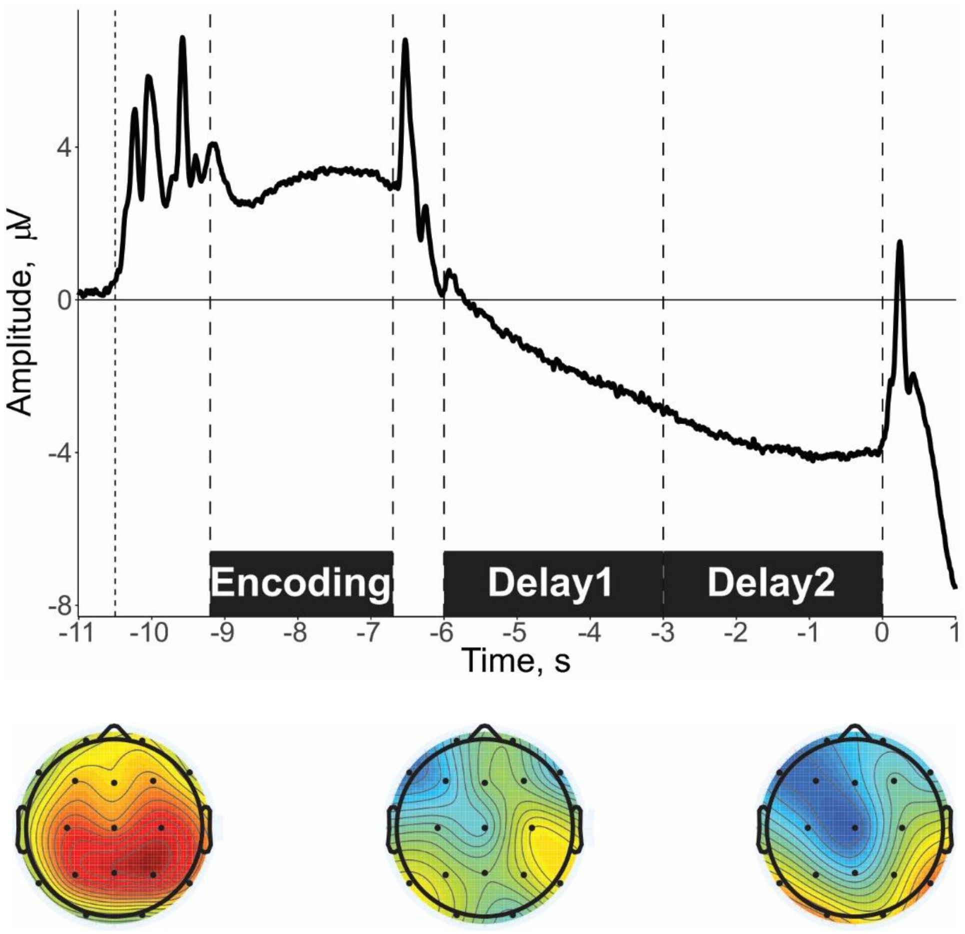

Figure 13 – Grand average waveforms of SCP over all conditions in Cz channel. Time intervals used in SCP and time-frequency analyses are marked with black boxes. Topographical plots in the bottom panel represent grand average SCP in Encoding, Delay1, and Delay2, respectively.

2.3.3 Time-frequency analysis

Before the time-frequency analysis, 1 Hz high-pass, 45 Hz low-pass and 50 Hz notch filters were applied. Epochs with the same properties as in SCP analysis were extracted.

The EEG time series in each epoch were convolved with a set of complex Morlet wavelets. The wavelets were defined as the product of a complex sine wave and a Gaussian window – $e^{-i2\pi tf}e^{-t^2/(2\sigma^2)}$, where t is time, f is frequency. σ is the width of the Gaussian, which set according to *n/(2πf)*, where *n* is the number of cycles – the parameter defining the time-frequency precision trade-off. The frequency *f* increased from 1 to 45 Hz in 45 linearly spaced steps, and the number of cycles *n* increased from 3 to 12 in 45 logarithmically spaced steps. From the resulting complex signal, the power of each frequency at each time point was obtained. The power was baseline-normalized by computing the percent change of the power in respect to [-11500 - 10500] ms interval – the same baseline interval as used in SCP analysis.

In order to decrease the number of factors employed in statistical calculations I defined frequency-channels regions of interest with maximal representation of certain frequencies in certain group of channels. Thus, theta (4-8 Hz) had the maximal power in Fz (see Figure 14), alpha (9-14 Hz) in posterior channels (T5, T6, P3, P4, O1, O2) (see Figure 15) and beta (16-22 Hz) in central channels (C3, Cz, C4) (see Figure 16).

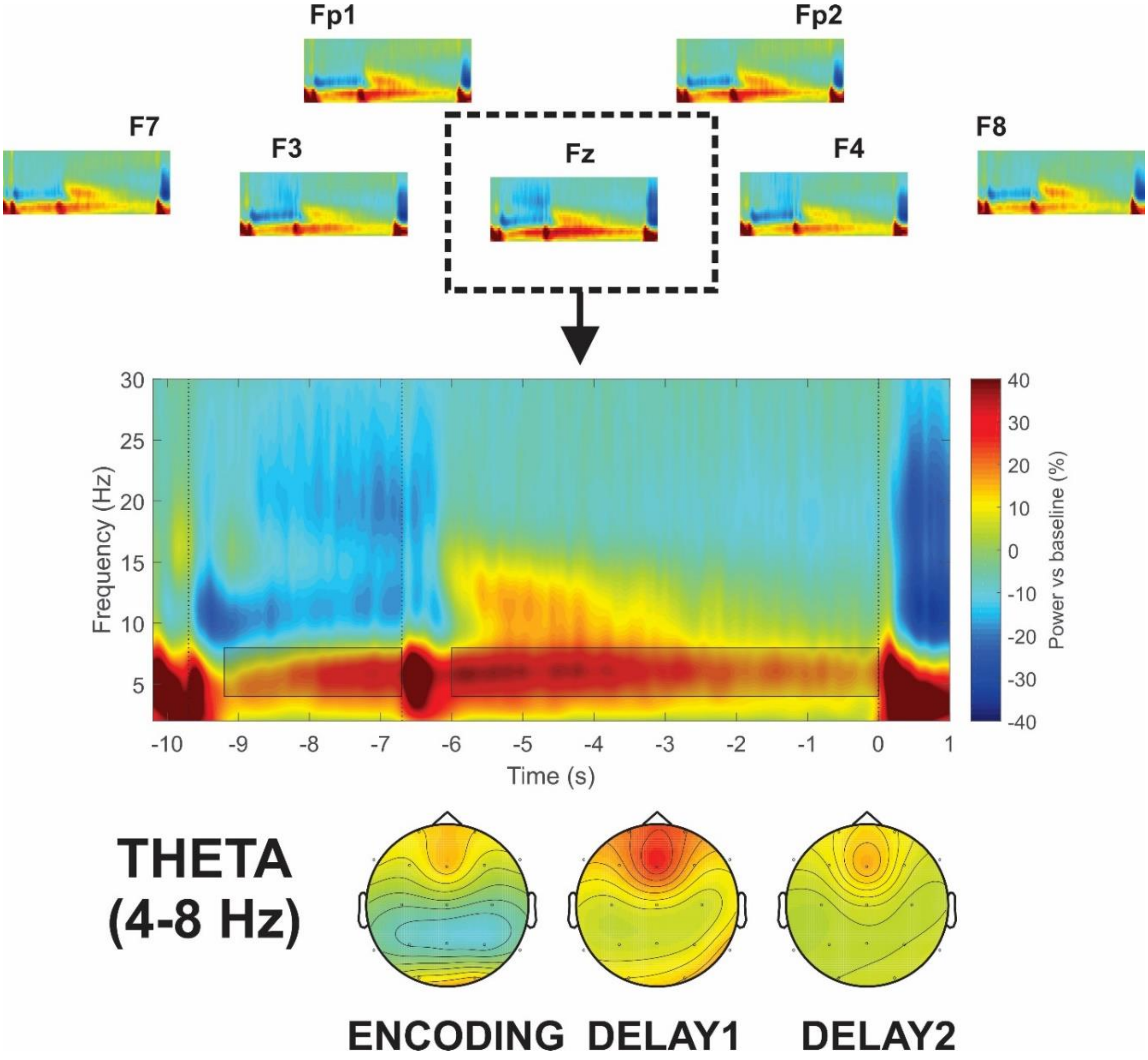

Figure 14 – Top panel: Time-frequency maps in individual channels. The power scale is the same as in the middle panel and bottom panels. Middle panel: Fz theta grand average. Two boxes mark the time windows: Encoding and Delay (Delay1 and Delay2 are combined here). Bottom panel: Topographical maps of averaged baseline-normalized theta (4-8 Hz) power in three time intervals. Two boxes mark the time windows: Encoding and Delay (Delay1 and Delay2 are combined here).

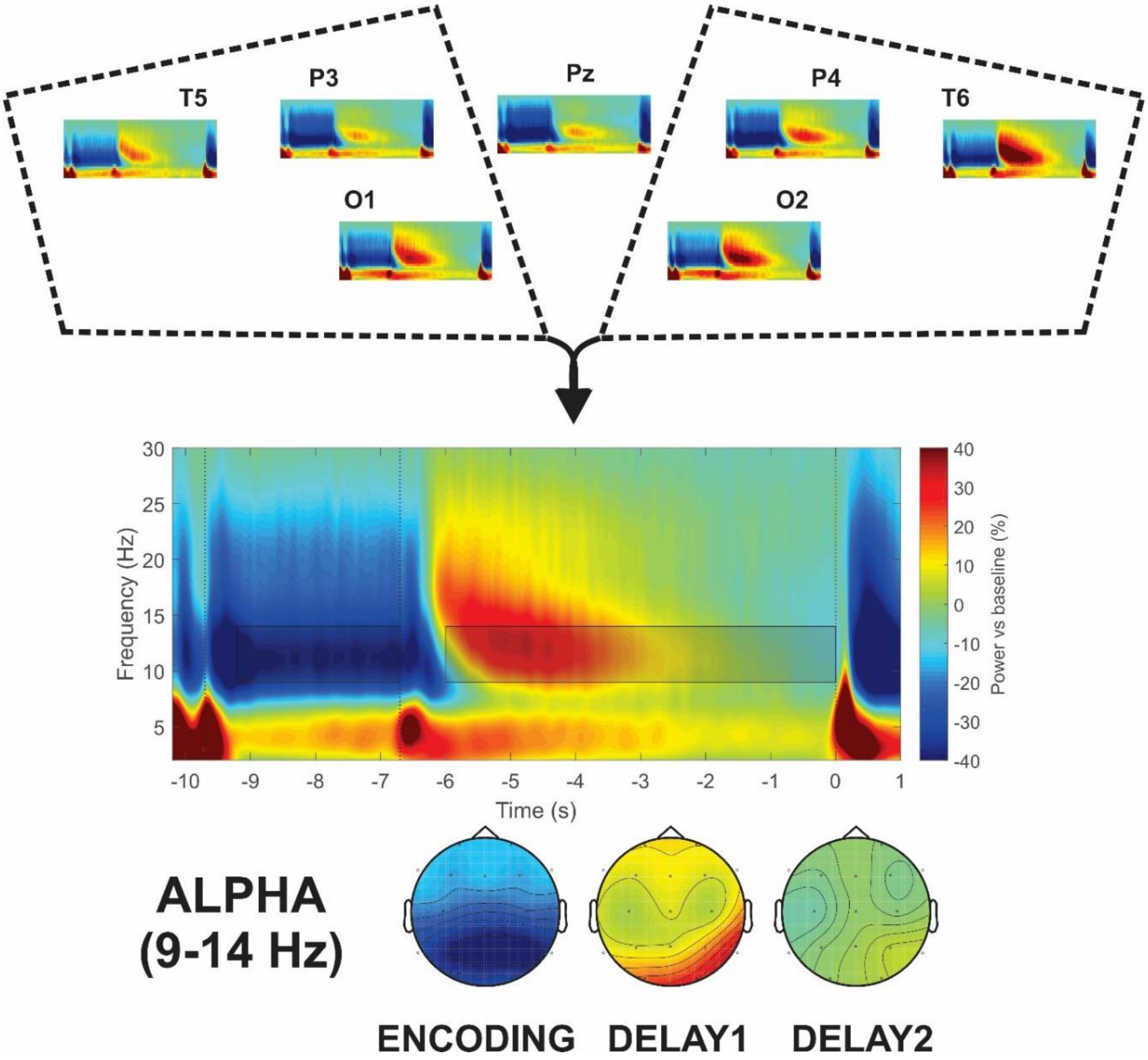

Figure 15 – Top panel: Time-frequency maps in individual channels. The power scale is the same as in the middle and bottom panels. Middle panel: Alpha ROI (Left: T5, P3, O1; Right: P4, T6, O2) grand average. Two boxes mark the time windows: Encoding and Delay (Delay1 and Delay2 are combined here). Bottom panel: Topographical maps of averaged baseline-normalized alpha (9-14 Hz) power in three time intervals.

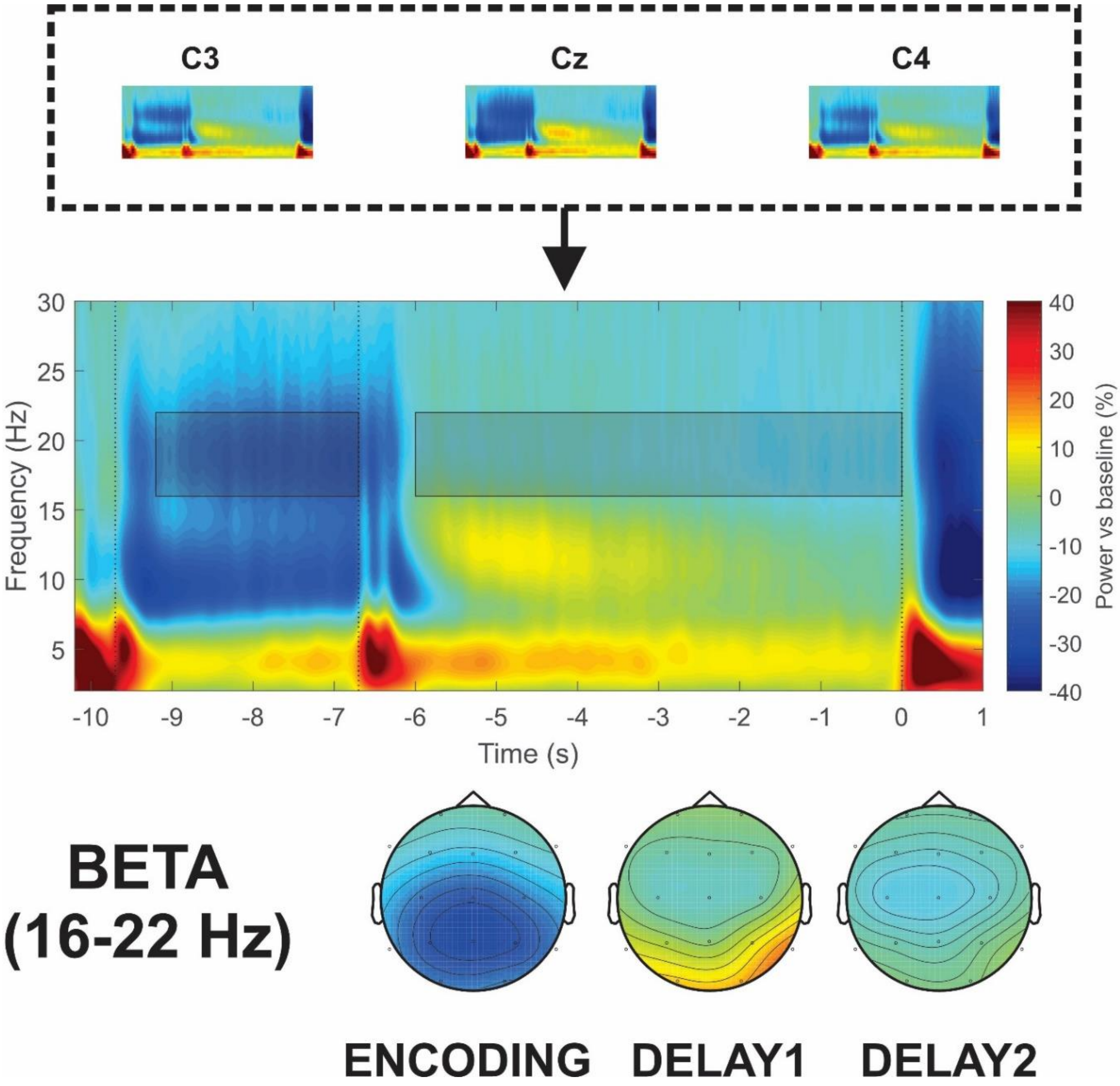

Figure 16 – Top panel: Time-frequency maps in individual channels. The power scale is the same as in the middle panel and bottom panels. Middle panel: Beta ROI (C3, Cz, C4) grand average. Two boxes mark the time windows: Encoding and Delay (Delay1 and Delay2 are combined here). Bottom panel: Topographical maps of averaged baseline-normalized beta (16-22 Hz) power in three time intervals.

As can be seen in Figure 15 alpha activity distributes beyond the conventional 8-13 Hz frequency band. Similar power leakage to the frequencies normally attributed to beta has been observed in other WM studies. A high frequency posterior alpha beyond classic frequency band limits (11-15 Hz) was used in a verbal WM study by Kustermann, Popov, et al. (2018). In another study 9-16 Hz frequency band was identified as alpha during encoding (Heinrichs-Graham & Wilson, 2015). However, it shifted to 10-13 Hz range during delay. In the study by Wianda & Ross (2019) a wide range 9-16 Hz alpha (alpha/beta) increase in the delay period was observed. Another work employing a visual WM task also evoked a stunningly similar to my study alpha effect in posterior channels (see Figure 17) (Johnson, Sutterer, Acheson, Lewis-Peacock, & Postle, 2011). Johnson et al. used mean alpha power in 8-15 Hz frequency band. Some authors prefer to use the classic 8-13 Hz for the statistical inference even though it is not justified by the observed data (e.g. Okuhata et al., 2013). My choice was to define alpha frequency band as one occupying frequencies between 9 and 14 Hz. Anyhow, changing the upper limit up to 18 Hz did not substantially change the statistical output or any of the conclusions.

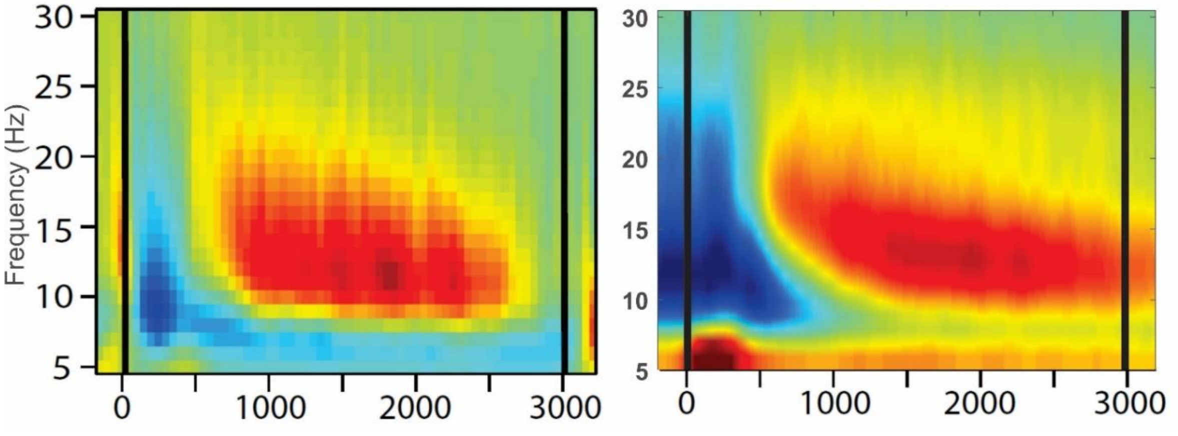

Figure 17 – Left panel: time-frequency representation of delay alpha activity in posterior EEG channels reported in Figure 3B in Johnson et al. (2011). Right panel: alpha activity in my study in the first 3 s of the delay period averaged in similar channels scaled to be comparable with the left panel figure.

For the statistical analyzes described in the following sections, the EEG power in theta, alpha and beta frequency bands was averaged in three time intervals. The time intervals are the same as those used in the SCP analysis. I excluded the initial 500 ms from the onset of Encoding as well as the initial 700 ms from the onset of Delay period. As can be seen in Figure 13 the first few hundred milliseconds after the onset of the delay and encoding onset contain evoked response activity that could distort the frequency data if not rejected (Ikkai et al., 2014; van Gerven et al., 2009; see also Figure 35).

2.4 Statistics

A large number of published results in psychology are likely false positives (Ioannidis, 2005; Simmons, Nelson, & Simonsohn, 2011). In order to address this problem in my dissertation, I have made the decision to minimize the probability of Type I error as much as possible, of course with the cost of paying much less attention to the probability of Type II error. First of all, I decided to use the alpha level of 0.005, as such a threshold exhibits higher evidential value and may also help to improve reproducibility of newly discovered effects (e.g. see Benjamin et al. (2018) but also Miller & Ulrich (2019) for another opinion). Most of the following statistical decisions are based on this ideology, including the rather large for psychophysiological experiments sample size and the use of mixed-effects models on the basis of single trials data to explore individual differences.

Psychology has a long tradition to evaluate findings based on significance testing and p-values. Effect sizes are less frequently reported and attract less attention (Fritz, Morris, & Richler, 2012), and often misinterpreted (Funder & Ozer, 2019). Even small and practically insignificant effect size can be associated with statistically significant effects. It is especially true when the sample size is large. Therefore, I used a combined approach to emphasize the importance of both measures. In the following ANOVAs, asterisks will be used to highlight the effects of different magnitude with partial eta squared equal to or larger than .0099*, .0588**, and .1379*** as benchmarks for small*, medium**, and large*** effect sizes, respectively (Cohen, 1992; Richardson, 2011). Effect size is marked in the statistical output tables only in the case of statistical significance ($p<0.005$).

All statistical calculations were performed in *R,* version 3.5.1 (R Core Team, 2013).

In the statistical analyses of EEG data, I employed two main approaches. First, I explored the general effects by application of well-known widely used repeated measures analysis of variance (ANOVA RM). Second, I took advantage of a relatively new for cognitive neuroscience statistical approach, namely linear mixed effects models (LMM) that, as will be shown later, is more suitable for studying individual differences.

2.4.1 General effects

In order to explore the effects of experimental condition on ERPs, ANOVA RM with within-subject factors Task (2 levels: Retention or Manipulation), Load (5, 6 or 7 letters to memorize) and Channel (Fz, Cz, Pz) was employed. Three most commonly used channels in ERP research were included to the analysis for two reasons. First, to increase the comparability with previous works using similar tasks; and second, because I did not expect any specific spatial effects in ERPs in lateral electrodes. The analysis was repeated for each of the extracted time windows (see Figure 12): Encoding P3a and P3b; Delay P2, P3a and P3b; Retrieval P3a and P3b.

In addition to Task and Load, a factor Time interval (TimeInt for short; with 3 levels: Encoding, Delay1 and Delay2) was used in ANOVAs employed to test the effects on the SCP amplitude. The analysis was repeated twice. The first ANOVA involved the three midline electrodes commonly used in ERP analyses (factor Channel with 3 levels: Fz, Cz, Pz). SCP may represent general activation-suppression cortical patterns and show local effect. To account for this possibility, in the second ANOVA I included two spatial factors instead of one: Hemisphere (Left: Fp1, F3, F7, O1, T5, P3; Right: F8, F4, Fp2, P4, T6, O2 electrodes) and Anterior-Posterior (AntPos, Anterior or Posterior regions of interest (ROI)). Anterior ROI comprised of Fp1, F3, F7, F8, F4, Fp2 channels and Posterior ROI included O1, T5, P3, P4, T6, O2 channels.

In order to test general effects in the time-frequency analysis, an ANOVA with factors Task, Load and TimeInt was used. This analysis was conducted separately for theta and beta frequency bands. To analyze alpha activity an additional factor Hemisphere (2 levels: Left (P3, T5, O1), Right (P4, T6, O2)) was used.

The percentage of correct answers and mean reaction time (RT) were used for behavioral data analysis with two factors: Load and Task.

Simple effects in ANOVA interactions were further explored with paired t-tests. The Holm method for correction for multiple comparisons was used where applicable.

2.4.2 Individual differences

A typical approach to EEG data analysis in the context of individual differences is to average the data within conditions, to split the sample into groups and to calculate an ANOVA with a between-subject factor Group. Splitting a continuous variable such as accuracy in a WM task into levels of a factor strongly reduces statistical power and might conceal non-linear effects in the data (Baayen, 2004; MacCallum, Zhang, Preacher, & Rucker, 2002). In order to overcome this problem, I used linear mixed-effects models (LMM, also known as multi-level models (MLM)) to study individual differences in working memory.

The first advantage of LMM is its ability to work equally with continuous and categorical independent variables. Second, unlike ANOVA RM, LMM allow to use more than one observation per cell, i.e. not mean spectral power in each condition but all trials and spectral power in single trials. In an ANOVA each participant's data has the same weight in the calculations. However, as a results of data preprocessing and artifact rejection some trials are removed. It leaves a researcher with an unequal number of data points contributing to the average on the single participant level. LMM are able to take into account the number of trials contributing to the within condition average.

The structure of LMM can be divided into two main parts: fixed and random effects. Fixed effects can generally be treated as factors in a typical ANOVA RM. They include the intercept (b0), which is the grand mean of all participants and conditions, as well as estimates of the effects of experimental conditions and their interactions. Random effects include random intercepts that can be seen as a grouping variable – most frequently it is subject. Subject intercept shows the difference of each individual from the group intercept. The strength of the effects can also vary inside each subject which is specified by inclusion of the random slopes to the model. For example, the power of alpha rhythm can be increasing with load in one subject but decreasing in another.

The so called maximal model random effects structure would include all by-subject random slopes and their interactions (Barr, Levy, Scheepers, & Tily, 2013). However, fitting a LMM is an iterative probabilistic procedure and it creates the main limitation of the approach – the model does not always converge on a solution (Eager & Roy, 2017). The convergence of the model depends primarily on the complexity of the random effects structure. As a rule, inclusion of random slopes and interaction terms to the model decreases the chances for the model to converge. As recommended by Barr et al. (2013), first, I always tried to fit the maximal model. In the case of the convergence problem, I first tried to fit the model with main effect random slopes (no interactions). If it converged, next, I again followed the advice by Barr (2013) and reduced the maximal random effect structure keeping the highest-order interaction slope (e.g. Task x Load x TimeInt x Hemisphere for alpha rhythm) and slopes that showed significant interactions with Performance at the previous step.

For beta and theta rhythms the maximal model included Task, Load, Time interval, Performance and all possible interactions as fixed effects, Participant as a grouping random intercept effect, and combination of Task, Load, Time interval and their interactions as random slopes. For alpha activity fixed and random effects of Hemisphere were additionally included. Performance was calculated as the mean percentage of correct answers averaged over all conditions. In this case Performance plays the role of a personal trait and allows a straightforward interpretation of possible interactions with the other fixed effects.

Before fitting the models, continuous variables were centered around zero, and qualitative variables were effect coded. For example, an effect-coded variable Task (Manipulation vs Retention) would involve coding Manipulation condition as -1 and Retention as 1; similarly, effect-coded levels of Time interval would be Encoding = -1, Delay1 = 0 and Delay2 = 1. Centering a variable around zero involved subtracting the mean and scaling by dividing by standard deviation. These transformations help to increase chances of convergence, computing speed, and numerical accuracy, and allows to make interactions more meaningful (Cheng, Edwards, Maldonado-Molina, Komro, & Muller, 2010).

lme4 package (Bates, Maechler, Bolker, & Walker, 2014) and function lmer in *R* was used to fit the models. For the calculation of p-values I used lmerTest package (Kuznetsova, Brockhoff, & Christensen, 2017) with the default Satterthwaite's degrees of freedom approximation. The models formulas in the results section are written using the syntax of lme4 package to make them more comprehensible. For example, the formula for theta spectral power effects related to WM performance will be presented as follows:

*Power ~ TimeInt * Task * Load * Performance + (TimeInt*Load*Task |Participant)*

Power is the dependent variable. *TimeInt, Task, Load, Performance* before the parentheses are fixed effects; *TimeInt, Load, Task* in the parentheses on the left from | sign are random slopes; and *Participant* is random intercept, i.e., the grouping variable.

RESULTS

3.1 Behavior

3.1.1 Accuracy

The analyses of simple effects showed no difference between performance in the two most difficult tasks 6M and 7M as well between 7R and 5A. All the other pairwise differences were significant (see Table 2 for mean values and Figure 18 for the visual depiction). See Table 1 below for full statistical output of the accuracy analysis.

Table 1 – ANOVA RM of accuracy

	DF	*F*	*η^2*	*p*
Task	1, 155	431.8	0.736	**< 0.0001 *****
Load	2, 307	138.8	0.472	**< 0.0001 *****
Task:Load	2, 305	22.1	0.125	**< 0.0001 ****

** small ** medium *** large effect size and p<0.005*

Table 2 – Descriptive statistics for accuracy

Load	*Task*	*Mean % correct responses*	*SD*	*SE*
5	Manipulation	79.55	14.33	1.15
5	Retention	92.28	9.02	0.72
6	Manipulation	66.22	15.51	1.24
6	Retention	88.65	10.94	0.88
7	Manipulation	65.61	13.52	1.08
7	Retention	80.71	13.55	1.09

Notes: SD – standard deviation, SE – standard error

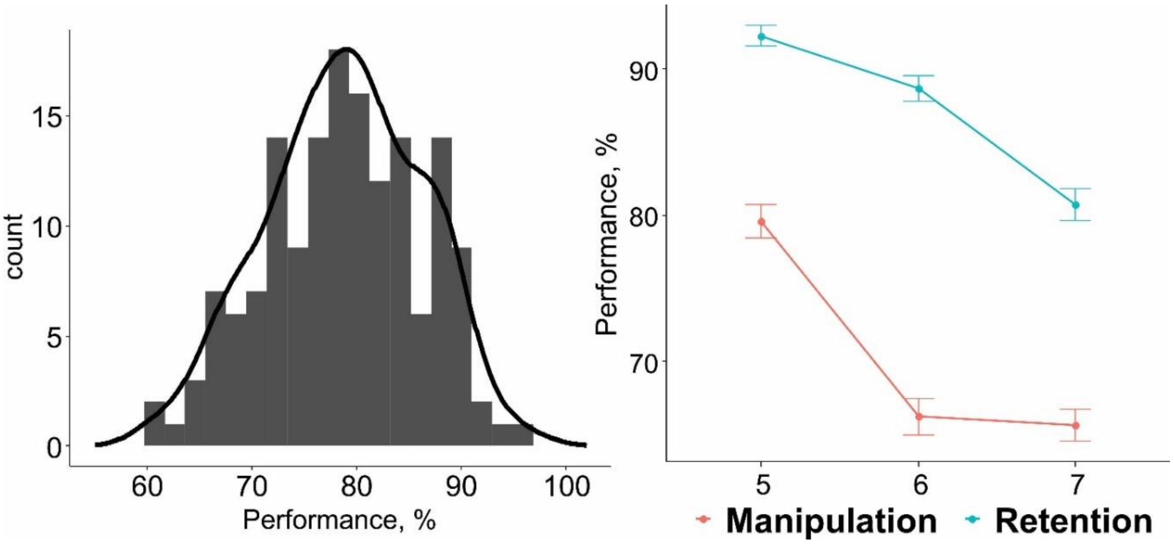

Figure 18 – Behavioral results. (A) Distribution of overall performance stacked into 25 bins. (B) Average performance in 6 conditions. Error bars are standard errors of the mean.

3.1.2 Reaction time

Reaction was significantly delayed in the manipulation condition as compared with the retention one (see Table 3 for full statistical output, Table 4 for mean values in each condition, Figure 19A for the distribution of the reaction times). Reaction time (RT) was longer in the higher load conditions. Pairwise comparisons of RT on the levels of load resulted in highly significant differences (all ts>49, ps<0.0001, see Figure 19B). The lack of a Task by Load interaction suggests that the dynamics of the slowing down with load effect was comparable in both tasks. The effect of correctness on RT (F(1,155) = 257, p < 0.0001, $\eta^2 = 0.62$) indicated that correct responses requiring less time to execute than errors (see Figure 19C). As a robustness check, using the median instead of the mean value yielded similar results, thus not affecting interpretation of the effects.

Table 3 – Reaction time ANOVA statistical output

	DF	*F*	η^2	*p*
Task	1, 155	54.99	0.26	**< 0.0001 *****
Load	2, 302	83.00	0.35	**< 0.0001 *****
Task:Load	2, 293	2.88	0.02	0.06054

** small ** medium *** large effect size and p<0.005*

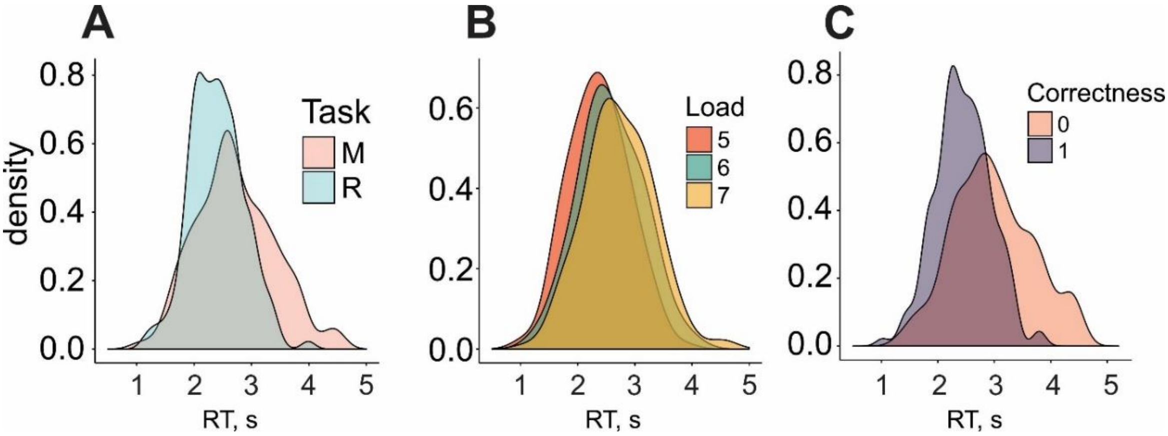

Figure 19 – Density plots of RT distribution. (A) Manipulation (M) and Retention (R) tasks' RT comparison. (B) Effect of Load on RT. (C) Effect of correctness of the responses on RT. 1 – correct responses, 0 – incorrect responses.

Table 4 – Reaction time descriptive statistics

Condition	*RT, s*	*SD*	*SE*
5 Manipulation	2.52	0.76	0.06
5 Retention	2.23	0.54	0.04
6 Manipulation	2.78	0.85	0.07
6 Retention	2.39	0.56	0.04
7 Manipulation	2.86	0.88	0.07
7 Retention	2.58	0.59	0.05

Notes: SD – standard deviation, SE – standard error

3.2 General tendencies

3.2.1 Event-related potentials

The results of ANOVA RM with factors Task, Load and Channel are presented in Table 5 and Figure 20.

Encoding P3a and P3b demonstrated similar anterior-posterior amplitude distribution, being the largest in Pz and smallest in Fz (main effect of Channel). The amplitudes of encoding P3a and P3b were smaller in Manipulation than in Retention task (main effect of Task). The effect of Task on P3a amplitude was the strongest at Pz ($t(155) = 4.28$, $p < 0.0001$, $d = 0.34$), still significant at Cz ($t(155) = 3.17$, $p = 0.002$, $d = 0.26$) and lost significance at Fz ($p = 0.57$). The task effect in the P3b time windows yielded significance only in the Pz channel (t(155) = 5.43, p < 0.0001, d = 0.44; Fz, p = 0.48 and Cz, p = 0.009).

The amplitude of *Delay* P2 was larger in the conditions with higher WM load (main effect of Load). The effect of Load was significant in all channels being the strongest in Cz (F(2, 310) = 13.8, η^2 = 0.082, p < 0.0001) and still significant in the other two channels (F(2, 310) = 8.04, η^2 = 0.049, p = 0.0004 in Fz; F(2, 306) = 6.79, η^2 = 0.042, p = 0.001 in Pz). Pairwise comparisons between levels of the factor Load in all three channels showed the same picture. The main effect of Load was driven by the difference between the 7 letters level of load and the others (7 vs 6: p = 0.0001; 7 vs 5: p<0.0001). No difference between the 6 and 5 letters levels of load was significant (p = 0.88). Delay P3a and P3b had a similar amplitude distribution, increasing from the front to the back (main effects of Channel). Tests of the Task effect in Channels in P3a time window showed no significant effects (all comparisons with p > 0.05), suggesting that the interaction Channel x Task was driven mainly by the strong main effect of Channel.

Retrieval P3a and P3b had the maximal amplitude at Pz (main effect of Channel). P3a and P3b had a larger amplitude in Manipulation task (main effect of Task). Despite the posterior nature of P3b the effect of Task was the strongest in Fz (Task x Channel interaction and Task effect in Fz: t(155) = 9.37, p < 0.0001, d = 0.75), became weaker in Cz (t(155) = 6.75, p < 0.0001, d = 0.54) and lost its significance in Pz (p = 0.036). P3b increased with set-size (main effect of Load). Only the difference between the 5 and 7 letters conditions was significant (t(155) = 3.77, p = 0.0002, d = 0.30; p > 0.01 in the other comparisons).

Table 5 –Condition effects statistics ERP

		DF	*F*	*pes*	*Pr(>F)*
ENCODING					
P3a	Load	2, 309	1.016	0.007	0.363
	Task	1, 155	9.446	0.057	**0.0025**
	Channel	2, 259	23.284	0.131	**< 0.0001 ****
	Load:Task	2, 309	2.242	0.014	0.108
	Load:Channel	3, 529	1.137	0.007	0.336
	Task:Channel	2, 266	7.884	0.048	**0.0009**
	Load:Task:Channel	2, 356	1.166	0.007	0.317

P3b	Load	2, 309	2.152	0.014	0.118
	Task	1, 155	8.272	0.051	**0.0046**
	Channel	2, 269	172.438	0.527	**< 0.0001 *****
	Load:Task	2, 310	0.985	0.006	0.374
	Load:Channel	3, 515	0.297	0.002	0.847
	Task:Channel	2, 247	23.098	0.130	**< 0.0001 ****
	Load:Task:Channel	2, 348	0.904	0.006	0.416
DELAY					
P2	**Load**	2, 308	10.958	0.066	**< 0.0001 ****
	Task	1, 155	4.695	0.029	0.032
	Channel	2, 245	32.374	0.173	**< 0.0001 *****
	Load:Task	2, 306	0.104	0.001	0.899
	Load:Channel	3, 515	4.395	0.028	**0.0033 ***
	Task:Channel	2, 262	5.886	0.037	0.0052 ·
	Load:Task:Channel	3, 466	0.192	0.001	0.902
P3a	Load	2, 308	1.498	0.010	0.225
	Task	1, 155	1.292	0.008	0.257
	Channel	2, 237	87.072	0.360	**< 0.0001 *****
	Load:Task	2, 300	0.446	0.003	0.634
	Load:Channel	3, 499	0.676	0.004	0.578
	Task:Channel	2, 274	9.671	0.059	**0.0002 ****
	Load:Task:Channel	3, 448	0.092	0.001	0.96
P3b	Load	2, 299	0.288	0.002	0.742
	Task	1, 155	0.027	0.000	0.869
	Channel	2, 246	101.408	0.396	**< 0.0001 *****
	Load:Task	2, 296	0.152	0.001	0.849
	Load:Channel	3, 503	0.271	0.002	0.86
	Task:Channel	2, 274	4.078	0.026	0.022
	Load:Task:Channel	3, 490	1.165	0.007	0.323
RETRIEVAL					
P3a	Load	2, 309	0.424	0.003	0.654
	Task	1, 155	8.806	0.054	**0.003 ***
	Channel	1, 209	14.339	0.085	**< 0.0001 ****
	Load:Task	2, 309	1.352	0.009	0.26
	Load:Channel	3, 487	1.918	0.012	0.123
	Task:Channel	2, 261	4.810	0.030	0.013
	Load:Task:Channel	3, 468	1.185	0.008	0.315
P3b	**Load**	2, 306	7.626	0.047	**0.0006 ***
	Task	1, 155	46.670	0.231	**< 0.0001 *****
	Channel	1, 209	492.427	0.761	**< 0.0001 *****

	Load:Task	2, 309	2.103	0.013	0.124
	Load:Channel	3, 472	1.608	0.010	0.186
	Task:Channel	2, 246	36.837	0.192	**< 0.0001 *****
	Load:Task:Channel	3, 492	2.304	0.015	0.073

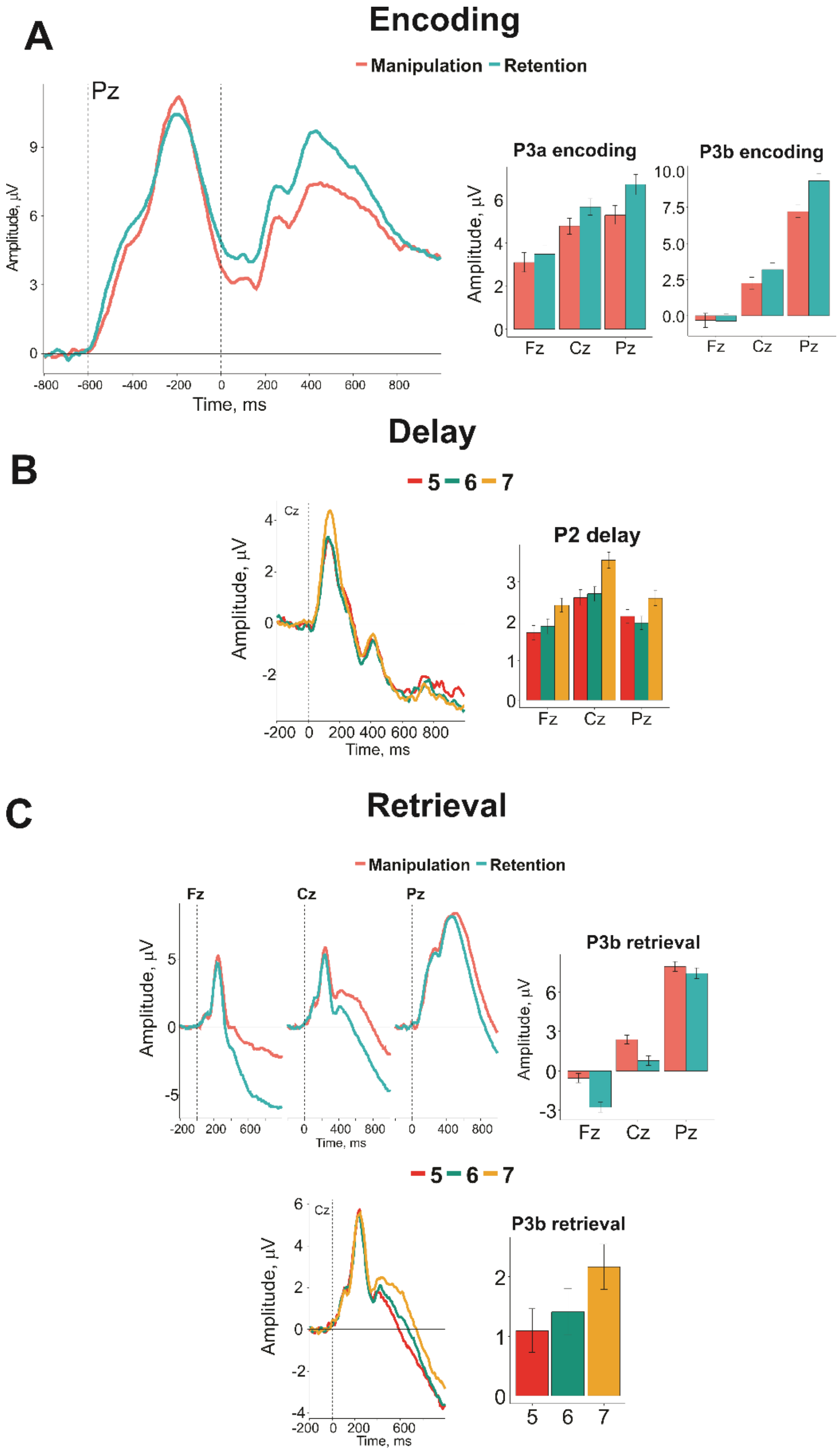

Figure 20 – Condition-related effects on ERPs. (A) The effect of Task at the Encoding stage. (B) The effect of Load on the P2 amplitude at the Delay stage. (C) The effects of Task and Load at the Retrieval stage. Error bars are the standard errors of the mean.

3.2.2 Slow cortical potentials

The ANOVA in the midline electrodes revealed that SCP in the manipulation task were more negative than in the retention one (main effect of Task, see Figure 21A,B and Figure 22A, full statistical output is in Table 6). It was the only one condition-related effect found in the SCP analyses. The comparison between SCP at different levels of load is shown in Figure 22B. The figure depicts no difference between the levels of load at any time point during encoding as well as during delay period.

The topographical maps showed left frontal and midline central distribution of SCP (see Figure 13). SCP averaged over all conditions and channels were positive during encoding but negative during delay (main effect of Time interval). Encoding SCP had clear posterior distribution with the maximum at Pz and switched to the maximum at Cz during delay (Channel x Time interval interaction, see Figure 21C,D).

To further explore the spatial distribution of SCP, another analysis in four ROIs was conducted. SCP were more negative in the left hemisphere (main effect of Hemisphere). SCP remained positive over time at the posterior sites and switched to negativity during delay at the anterior sites (main effect of Time interval, Time interval x Anterior-Posterior interaction, Figure 21E,F). The difference between SCP over the left and right hemispheres as revealed by simple effects analyses of the Time interval x Anterior-Posterior x Hemisphere interaction was present during encoding at the posterior sites ($t(155) = 4.56$, $p < 0.0001$, $d = 0.37$) and during delay at the anterior sites (Delay1: $t(155) = 2.83$, $p = 0.0052$, $d = 0.23$; Delay2: $t(155) = 3.59$, $p = 0.0004$, $d = 0.29$; $p>0.1$ in all other comparisons).

Table 6 – Slow cortical potentials ANOVA statistical output

	DF	*F*	η^2	*p*
Load x Task x TimeInt x Channel (Fz, Cz, Pz)				
Channel	2, 272	4.060	0.026	0.023
Task	1, 155	11.644	0.070	**0.0008**
Load	2, 283	0.105	0.001	0.884
TimeInt	2, 266	52.635	0.253	**< 0.0001**
Channel:Task	2, 292	0.971	0.006	0.376
Channel:Load	3, 541	0.531	0.003	0.689
Task:Load	2, 310	0.010	<0.001	0.990
Channel:TimeInt	3, 410	7.396	0.046	**0.0002**
Task:TimeInt	2, 252	5.923	0.037	0.006 ·
Load:TimeInt	3, 452	0.289	0.002	0.828
Channel:Task:Load	3, 532	0.704	0.005	0.568
Channel:Task:TimeInt	3, 484	0.339	0.002	0.805
Channel:Load:TimeInt	6, 939	1.517	0.010	0.169
Task:Load:TimeInt	3, 478	0.628	0.004	0.602
Channel:Task:Load:TimeInt	5, 739	1.362	0.009	0.239
AntPos x Hemisphere x Load x Task x TimeInt				
AntPos	1, 155	29.295	0.159	**< 0.0001**
Hemisphere	1, 155	9.200	0.056	**0.003**
Task	1, 155	0.395	0.003	0.531
Load	2, 301	0.438	0.003	0.640
TimeInt	1, 226	12.693	0.076	**< 0.0001**
AntPos:Hemisphere	1, 155	3.815	0.024	0.053
AntPos:Task	1, 155	0.355	0.002	0.552
Hemisphere:Task	1, 155	3.919	0.025	0.050
AntPos:Load	2, 304	0.308	0.002	0.731
Hemisphere:Load	2, 265	1.620	0.010	0.203
Task:Load	2, 277	0.285	0.002	0.728
AntPos:TimeInt	1, 227	17.910	0.104	**< 0.0001**
Hemisphere:TimeInt	2, 233	1.233	0.008	0.285
Task:TimeInt	2, 256	0.455	0.003	0.597
Load:TimeInt	2, 354	0.802	0.005	0.464
AntPos:Hemisphere:Task	1, 155	0.674	0.004	0.413
AntPos:Hemisphere:Load	2, 264	0.376	0.002	0.653
AntPos:Task:Load	2, 309	0.088	0.001	0.916
Hemisphere:Task:Load	2, 302	1.888	0.012	0.154
AntPos:Hemisphere:TimeInt	2, 261	20.392	0.116	**< 0.0001**
AntPos:Task:TimeInt	1, 214	5.638	0.035	0.010

Hemisphere:Task:TimeInt	2, 238	1.614	0.010	0.206
AntPos:Load:TimeInt	2, 287	0.358	0.002	0.683
Hemisphere:Load:TimeInt	3, 429	0.070	<0.001	0.970
Task:Load:TimeInt	3, 420	0.690	0.004	0.544
AntPos:Hemisphere:Task:Load	2, 291	0.019	<0.001	0.976
AntPos:Hemisphere:Task:TimeInt	2, 236	0.266	0.002	0.706
AntPos:Hemisphere:Load:TimeInt	2, 375	0.772	0.005	0.485
AntPos:Task:Load:TimeInt	2, 385	0.802	0.005	0.473
Hemisphere:Task:Load:TimeInt	3, 479	1.928	0.012	0.122
AntPos:Hemisphere:Task:Load:TimeInt	3, 417	1.426	0.009	0.237

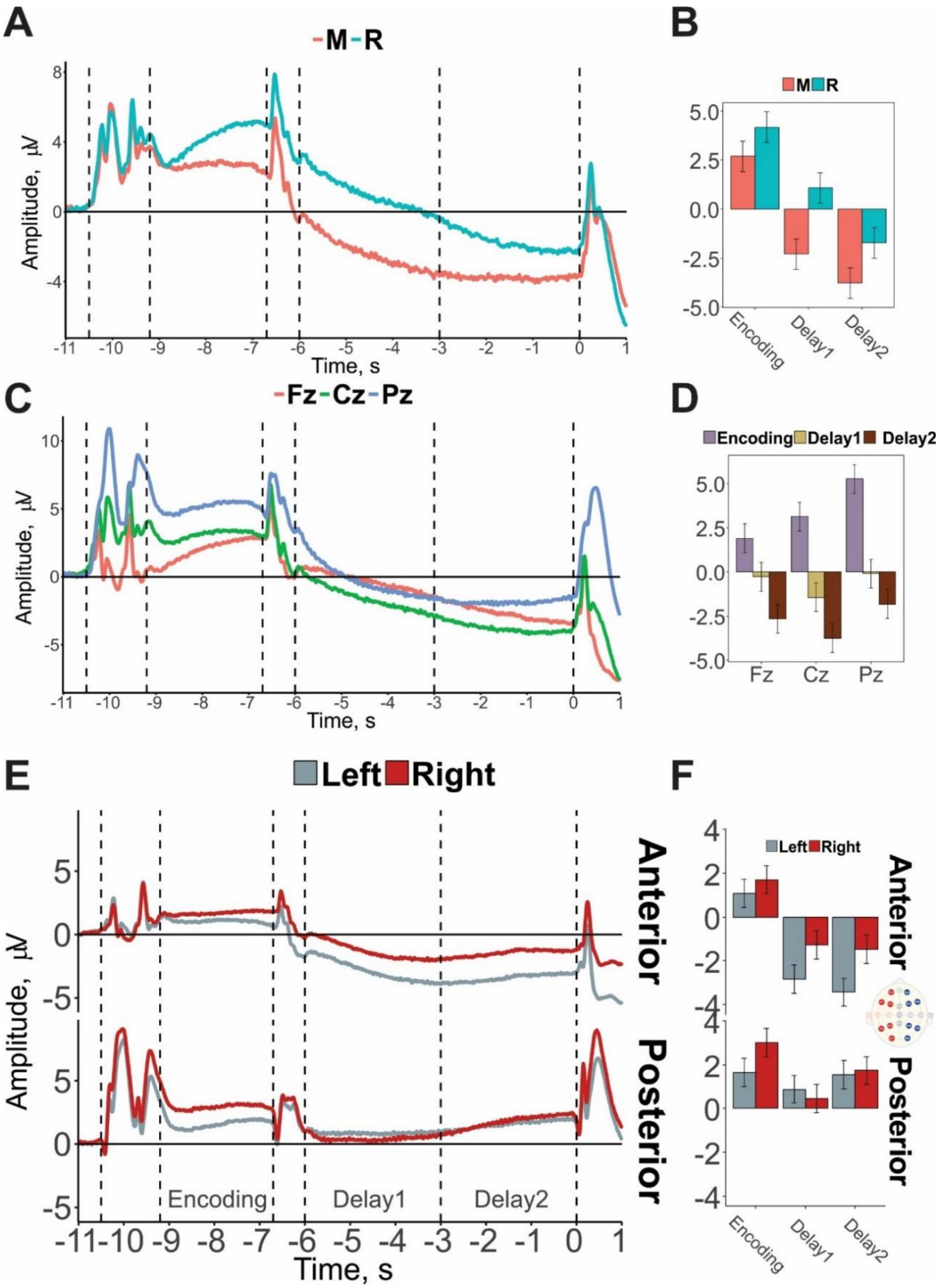

Figure 21 – Slow cortical potentials. (A, B) The effect of Task in three time intervals. (C, D) The effect of Channel on SCP in three time intervals. (E, F) Topographical distribution of SCP along the Left-Right and Anterior-Posterior axes. *Notes:* M – Manipulation task, R – Retention task. Error bars are the standard errors of the mean.

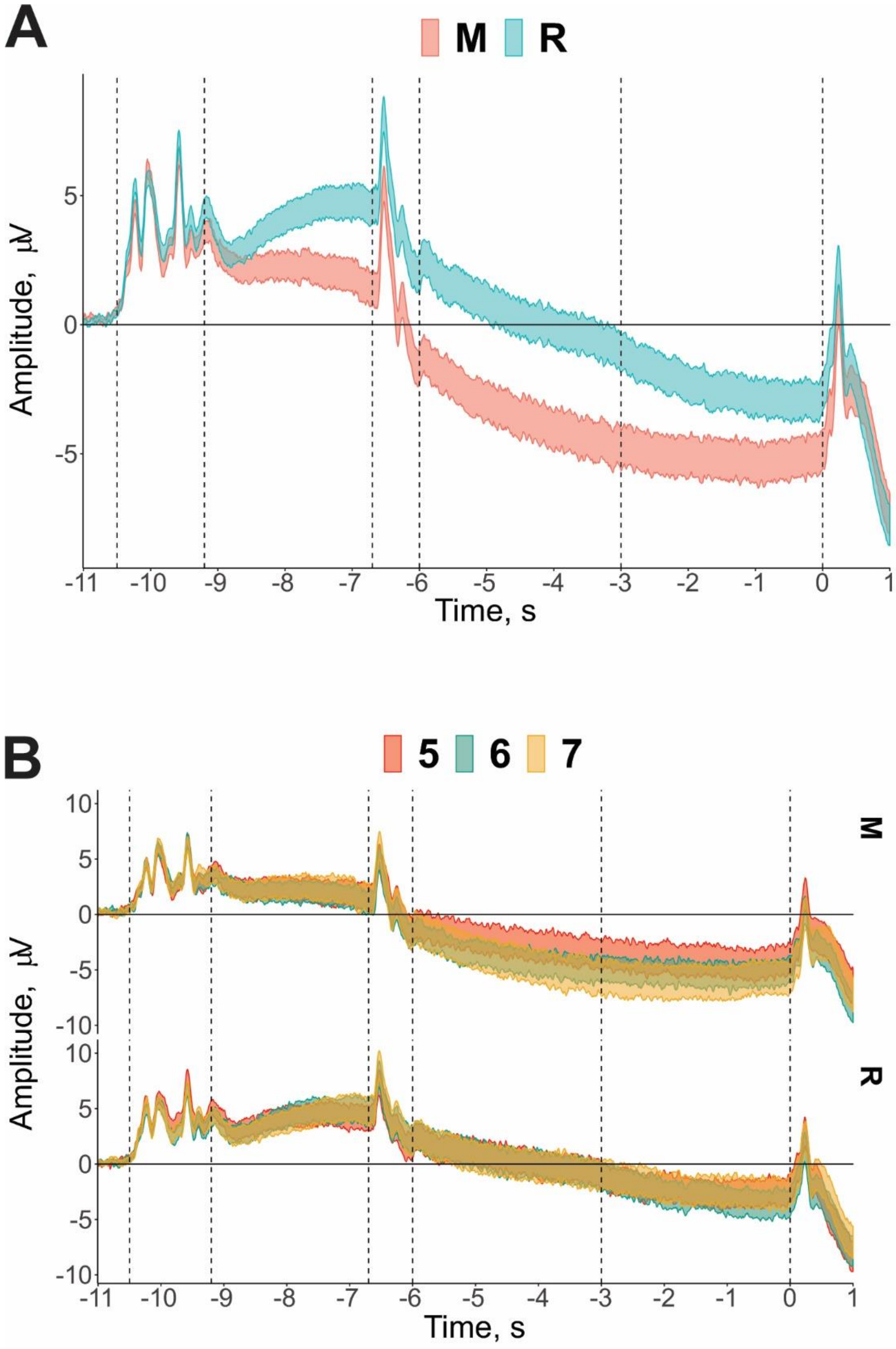

Figure 22 – SCP at the Cz electrode. (A) The effect of Task in time. (B) The effect of Load on SCP in Retention and Manipulation tasks. *Notes:* M – Manipulation task, R – Retention task. 5, 6, 7 – levels of load. Thickness of the lines represents mean ± SE.

3.2.3 Time-frequency analysis

3.2.3.1 Theta

General effects in the theta frequency band are summarized in Table 7. Theta activity was dependent on the time interval (main effect of TimeInt, see Figure 23). Specifically, the relative theta power was higher during encoding than during Delay1 (t(155) = 7.34, p < 0.0001, d = 0.59) but not significantly different from Delay2 (p = 0.27). The increase of theta in the first part of the Delay was stronger than in the second part (t(155) = 4.99, p < 0.0001, d = 0.40).

The theta increase was stronger in the manipulation as compared to the retention task (main effect of Task). This effect was modulated by time interval (TimeInt x Task interaction). The task effect was present during encoding (t(155) = 4.96, p < 0.0001, d = 0.40) and Delay1 (t(155) = 4.28, p < 0.0001, d = 0.34) but did not attain significance during Delay2 (p = 0.33).

Table 7 – ANOVA RM statistics in theta

	DF	*F*	*η^2*	*p*
TimeInt	2, 298	22.69	0.128	**< 0.0001 ****
Task	1, 155	17.16	0.100	**< 0.0001 ****
Load	2, 275	1.09	0.007	0.333
TimeInt:Task	2, 249	9.52	0.058	**0.0003 ***
TimeInt:Load	2, 341	1.45	0.009	0.236
Task:Load	2, 249	4.58	0.029	0.017
TimeInt:Task:Load	2, 326	1.85	0.012	0.157

** small ** medium *** large effect size and p<0.005*

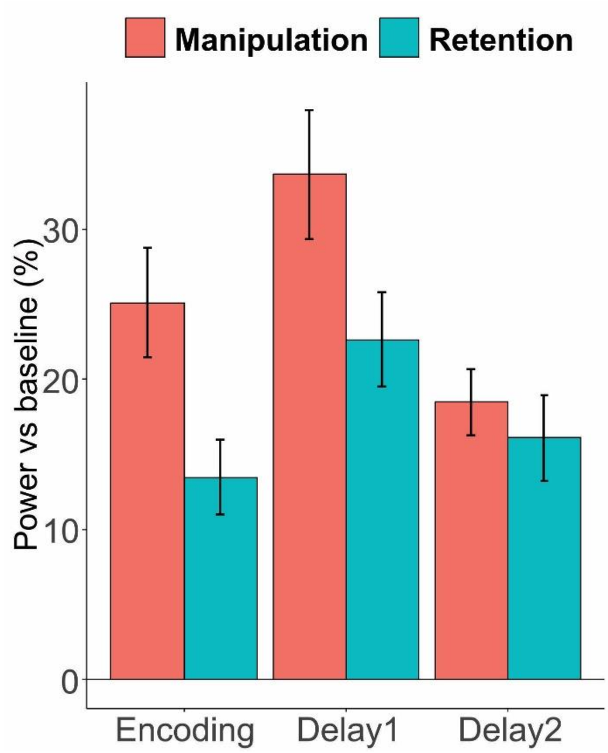

Figure 23 – General effects in theta frequency band. Time interval by Task interaction. Error bars are the standard errors of the mean.

3.2.3.2 Alpha

The results of ANOVA RM in alpha frequency band are summarized in Table 8. As illustrated in Figure 24, alpha activity was strongly affected by the time interval. After an initial suppression during encoding the pattern reversed in Delay1. In Delay2, the relative alpha power was not significantly different from the baseline level (t(155) = 0.84, p = 0.4, d = 0.07). As a result, alpha in Delay1 was significantly larger than in Delay2 (t(155) = 8.504, p < 0.0001, d = 0.68).

On average, the relative alpha power was larger in the right compared to the left hemisphere (main effect of Hemisphere). This effect was modulated by Time interval (TimeInt x Hemisphere interaction, see Figure 24A). The difference between alpha power in the left and right hemisphere during encoding (t(155) = 3.18, p = 0.002, d = 0.26) was not as strong as during the first (t(155) = 8.36, p < 0.0001, d = 0.67) and second part of the delay (t(155) = 5.57, p < 0.0001, d = 0.48). ANOVAs with two levels of TimeInt factor: either Encoding and Delay1 or Encoding and Delay2 resulted in significant TimeInt x Hemisphere interactions (Fs > 45, ps < 0.0001), confirming the stronger alpha asymmetry in the delay period compared with encoding. In order to check whether alpha asymmetry in the first part of the delay is stronger than in the second part, I reran the analysis using only the data from the delay period (factor TimeInt with 2 levels: Delay1 vs Delay2). The analysis resulted in a significant interaction Hemisphere x TimeInt ($F(1, 155) = 48.9$, $p < 0.0001$, $\eta^2 = 0.24$) confirming the hypothesis.

Table 8 – Alpha ANOVA RM

	DF	*F*	*η^2*	*p*
Hemisphere	1, 155	39.55	0.203	**< 0.0001*****
TimeInt	2, 263	222.36	0.589	**< 0.0001*****
Task	1, 155	7.66	0.047	0.006
Load	2, 304	0.73	0.005	0.479
Hemisphere:TimeInt	1, 222	64.15	0.293	**< 0.0001 *****
Hemisphere:Task	1, 155	4.69	0.029	0.032
TimeInt:Task	2, 246	5.55	0.035	0.008
Hemisphere:Load	2, 304	0.09	0.001	0.909
TimeInt:Load	3, 489	3.76	0.024	0.010
Task:Load	2, 301	2.22	0.014	0.112
Hemisphere:TimeInt:Task	2, 240	7.18	0.044	**0.002 ***
Hemisphere:TimeInt:Load	3, 490	1.43	0.009	0.230
Hemisphere:Task:Load	2, 307	0.19	0.001	0.829
TimeInt:Task:Load	3, 500	0.55	0.004	0.660
Hemisphere:TimeInt:Task:Load	3, 421	0.82	0.005	0.472

** small ** medium *** large effect size and p<0.005*

Although both alpha increase (delay) and suppression (encoding) were stronger in the right hemisphere, the effect of weaker alpha increase in the manipulation task appeared only in the left hemisphere (Hemisphere x TimeInt x Task interaction). In the left hemisphere the main effect of Task (i.e. Manipulation alpha < Retention alpha) was found during Delay1 ($t(155) = 3.82$, $p = 0.0002$, $d = 0.31$) and Delay2 ($t(155) = 3.558$, $p < 0.0001$, $d = 0.33$). In order to test whether the effect of Task was stable during delay I conducted another ANOVA using only the data in the left hemisphere and delay. No significant interaction TimeInt x Task was found ($p = 0.26$). In addition, to find more support for the lack of time related changes in the effect of Task, I conducted a Bayes ANOVA. For this analysis I used BayesFactor package for *R* with default priors. The resulting $BF_{01} = 7.3$ for TimeInt x Task interaction suggests that the model without the interaction is 7.3 times better supported by the data. The analyses support the idea that the effect of more suppressed alpha in the manipulation task during delay is stable over time (see Figure 24C).

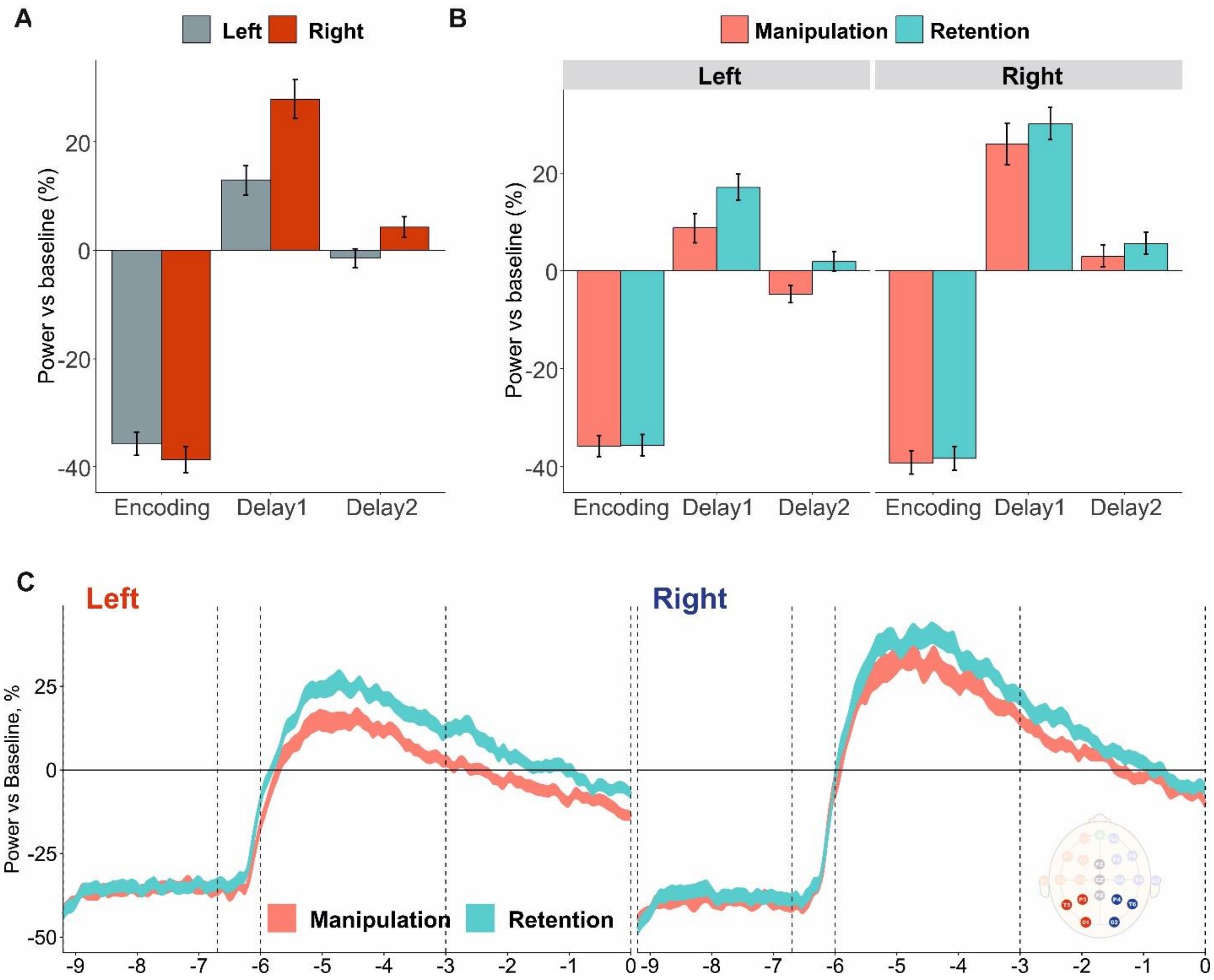

Figure 24 – General effects in alpha frequency band. (A) interaction Hemisphere x Time interval (B) interaction Hemisphere x Time interval x Task. Error bars show the standard errors of the mean. (C) Distribution of the relative power of alpha in time in the left and right hemisphere. Thickness of the lines represents mean ± SE.

3.2.3.3 Beta

The results of ANOVA RM in alpha frequency band are summarized in Table 9. The beta rhythm decreased during the task as compared with baseline, and this decrease was stronger in the manipulation condition than in the retention one (main effect of Task, see Figure 25). The encoding period was characterized by a stronger suppression of beta as compared to Delay, whereas beta was lower during Delay2 as compared with Delay1 (TimeInt main effect). Pairwise comparisons revealed strong effects distinguishing each level of the TimeInt factor (min t = 7.47, ps < 0.0001, min d = 0.60).

Subsequent t-tests to examine the TimeInt x Task interaction showed that beta was stronger suppressed in the manipulation task only during Delay1 ($t(155) = 4.9$, $p < 0.0001$, $d = 0.39$) but not during Encoding ($p = 0.35$) or Delay2 ($p = 0.011$ after Holm's correction).

The Task x Load interaction indicated a different load-dependent dynamics in Manipulation and Retention conditions (see Figure 25). Taking into account the lacking effects of Load in all previous comparisons, it was worth investigating this formally non-significant ($p = 0.0055$) interaction. Two omnibus ANOVAs with the factor Load in Manipulation and Retention conditions revealed no significant effects ($p = 0.04$ and 0.14 respectively).

Table 9 – Beta ANOVA RM

	DF	*F*	η^2	*p*
TimeInt	1, 224	182.38	0.541	**< 0.0001 *****
Task	1, 155	11.34	0.068	**0.001 ****
Load	2, 306	0.19	0.001	0.827
TimeInt:Task	2, 285	23.85	0.133	**< 0.0001 ****
TimeInt:Load	4, 580	0.63	0.004	0.628
Task:Load	2, 299	5.42	0.034	**0.0055 ·**
TimeInt:Task:Load	4, 579	1.48	0.009	0.210

** small ** medium *** large effect size and p<0.005,* · p = 0.0055

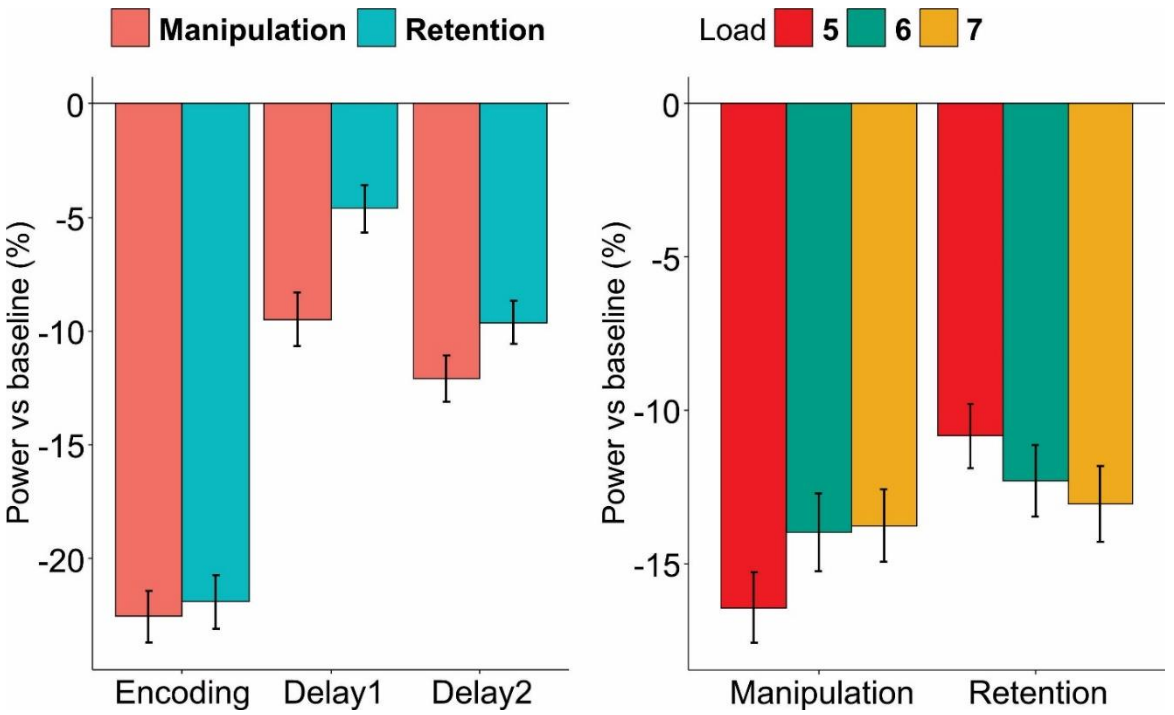

Figure 25 – General effects in beta frequency band. Left panel: Time interval by Task interaction. Right panel: Task by Load interaction.

3.3 Individual differences

3.3.1 Event-related potentials

Maximal models written as Amplitude ~ Task * Load * Channel * Performance + (Task * Load * Channel | Participant) successfully converged in analyzes of all ERP dependent variables. The statistical output is presented in Table 10.

Figure 26 (A, B) shows that larger amplitude of encoding P3b was related to better WM performance (Channel x Performance interaction). Although the correlation was stronger in Pz than in the other channels, it did not reach the criterion for statistical significance (Pz: r = 0.20, p = 0.009, Cz: r = 0.14, p = 0.079, Fz: r = -0.02, p = 0.84).

Similarly, retrieval P3b showed steeper slopes for the relationship between the 7 letters load and WM performance than in the other conditions (Load x Performance interaction, see Figure 26 (C,D)). However, no significant correlation between performance and P3b amplitude in the 7 letters load condition was observed (7 letters: r = 0.14, p = 0.08, 6 letters: r = 0.06, p = 0.46, 5 letters: r = -0.004, p = 0.95).

Table 10 – LMM condition-related effects

		β	*SE*	*t*	*p*
	ENCODING				
P3a	(Intercept)	0.0051	0.0203	0.25	0.802
	Performance	0.0297	0.0203	1.46	0.146
	Task:Performance	0.0119	0.0072	1.65	0.101
	Load:Performance	-0.0151	0.0096	-1.58	0.117
	Channel:Performance	0.0244	0.0094	2.58	0.011
	Task:Load:Performance	0.0079	0.0094	0.84	0.403
	Task:Channel:Performance	0.0005	0.0051	0.10	0.922
	Load:Channel:Performance	0.0025	0.0064	0.39	0.698
	Task:Load:Channel:Performance	-0.0001	0.0065	-0.02	0.983
P3b	(Intercept)	0.0045	0.0194	0.23	0.816
	Performance	0.0293	0.0194	1.51	0.134
	Task:Performance	0.0154	0.0075	2.05	0.042
	Load:Performance	-0.0186	0.0094	-1.97	0.050
	Channel:Performance	*0.0309*	*0.0097*	*3.18*	**0.002**
	Task:Load:Performance	0.0051	0.0098	0.52	0.605
	Task:Channel:Performance	-0.0034	0.0051	-0.66	0.512
	Load:Channel:Performance	0.0026	0.0063	0.41	0.683
	Task:Load:Channel:Performance	0.0047	0.0065	0.73	0.464
	DELAY				
P2	(Intercept)	-0.0002	0.0148	-0.01	0.989
	Performance	-0.0018	0.0148	-0.12	0.903
	Task:Performance	-0.0009	0.0076	-0.12	0.902
	Load:Performance	0.0073	0.0089	0.82	0.411
	Channel:Performance	-0.0045	0.0057	-0.78	0.438
	Task:Load:Performance	-0.0078	0.0095	-0.82	0.415
	Task:Channel:Performance	-0.0022	0.0052	-0.43	0.665
	Load:Channel:Performance	-0.0016	0.0063	-0.25	0.804
	Task:Load:Channel:Performance	0.0003	0.0063	0.05	0.957
P3a	(Intercept)	0.0010	0.0177	0.06	0.953
	Performance	-0.0214	0.0177	-1.21	0.228
	Task:Performance	-0.0086	0.0080	-1.08	0.281
	Load:Performance	-0.0019	0.0095	-0.20	0.840
	Channel:Performance	0.0065	0.0060	1.09	0.277
	Task:Load:Performance	-0.0057	0.0102	-0.56	0.576
	Task:Channel:Performance	-0.0081	0.0051	-1.59	0.113
	Load:Channel:Performance	0.0029	0.0062	0.47	0.642
	Task:Load:Channel:Performance	0.0004	0.0063	0.07	0.945

P3b	(Intercept)	0.0011	0.0157	0.07	0.944
	Performance	-0.0146	0.0157	-0.93	0.354
	Task:Performance	0.0097	0.0074	1.30	0.195
	Load:Performance	-0.0112	0.0091	-1.23	0.222
	Channel:Performance	-0.0040	0.0069	-0.58	0.566
	Task:Load:Performance	-0.0072	0.0093	-0.77	0.443
	Task:Channel:Performance	-0.0069	0.0051	-1.36	0.175
	Load:Channel:Performance	0.0060	0.0063	0.97	0.334
	Task:Load:Channel:Performance	0.0033	0.0063	0.52	0.603
RETRIEVAL					
P3a	(Intercept)	0.0007	0.0226	0.03	0.975
	Performance	0.0217	0.0226	0.96	0.338
	Task:Performance	0.0039	0.0079	0.49	0.622
	Load:Performance	0.0200	0.0090	2.23	0.027
	Channel:Performance	0.0076	0.0096	0.79	0.431
	Task:Load:Performance	0.0009	0.0090	0.10	0.921
	Task:Channel:Performance	0.0063	0.0050	1.25	0.210
	Load:Channel:Performance	-0.0076	0.0062	-1.22	0.222
	Task:Load:Channel:Performance	-0.0014	0.0061	-0.22	0.825
P3b	(Intercept)	0.0003	0.0243	0.01	0.989
	Performance	0.0152	0.0243	0.62	0.534
	Task:Performance	-0.0179	0.0083	-2.17	0.032
	Load:Performance	0.0269	0.0094	2.87	**0.005**
	Channel:Performance	0.0077	0.0105	0.73	0.464
	Task:Load:Performance	0.0024	0.0083	0.29	0.774
	Task:Channel:Performance	0.0128	0.0049	2.60	0.009
	Load:Channel:Performance	-0.0092	0.0061	-1.50	0.134
	Task:Load:Channel:Performance	0.0007	0.0060	0.11	0.910

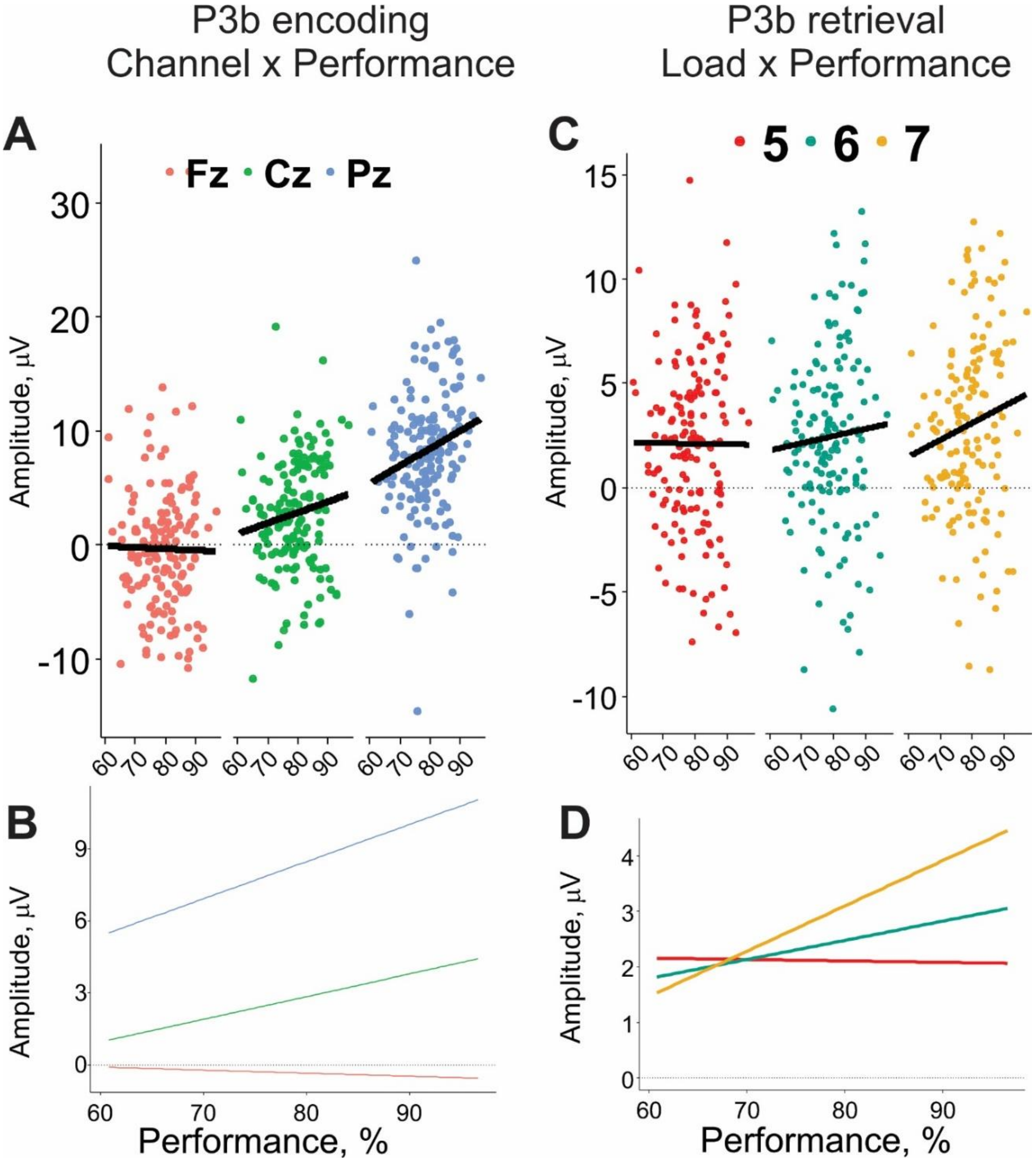

Figure 26 – (A) (B) Channel x Performance interaction in encoding P3b. (C) (D) Load x Performance interaction in retrieval P3b. Panels A and C show point diagrams, where each point represents a subject. Panels B and D show the corresponding slopes.

3.3.2 Slow cortical potentials

No significant effects relating Performance and SCP were found in this analysis (see Table A3 in the appendix).

3.3.3 Time-frequency analysis

3.3.3.1 Theta

The maximal model for theta successfully converged. The model's description:

*Power ~ TimeInt * Task * Load * Performance + (TimeInt*Load*Task |Participant)*

See Table 11 for LMM of theta statistical output.

Table 11 - Theta statistics in LMM

	β	*SE*	*t*	*p*
(Intercept)	21.63	2.50	8.67	< 0.0001
Performance	-0.71	2.50	-0.28	0.777
TimeInt:Performance	-0.39	0.91	-0.43	0.669
Task:Performance	*-3.00*	*0.99*	*-3.03*	**0.003**
Load:Performance	1.24	0.75	1.64	0.103
TimeInt:Task:Performance	-0.38	0.70	-0.54	0.591
TimeInt:Load:Performance	0.60	0.53	1.13	0.261
Task:Load:Performance	-1.17	1.46	-0.80	0.423
TimeInt:Task:Load:Performance	-1.49	0.62	-2.39	0.018

For the ease of data interpretation and illustration purposes the whole sample was split into the high performance (N = 78) and low performance (N = 78) groups. The groups were median-split on the basis of their average performance across all conditions.

Time-frequency maps representing changes in spectral power of low performance and high performance groups in two tasks are shown in Figure 27A,B. The figures show a strong increment of theta activity during task performance. As can be seen, the high performance group was characterized by a stronger theta increase in Manipulation task. This observation was confirmed by a positive association between the relative theta power and behavioral performance in the Manipulation task and a negative association with performance in the simple Retention task (see Figure 27C). Then, I correlated WM performance with the difference between theta in Manipulation and Retention tasks to test the hypothesis on the role of executive components of WM in individual differences. The larger was the difference between baseline normalized theta power in Manipulation and Retention conditions, the better the individual WM performance (r = 0.24, p = 0.003) (see Figure 27D).

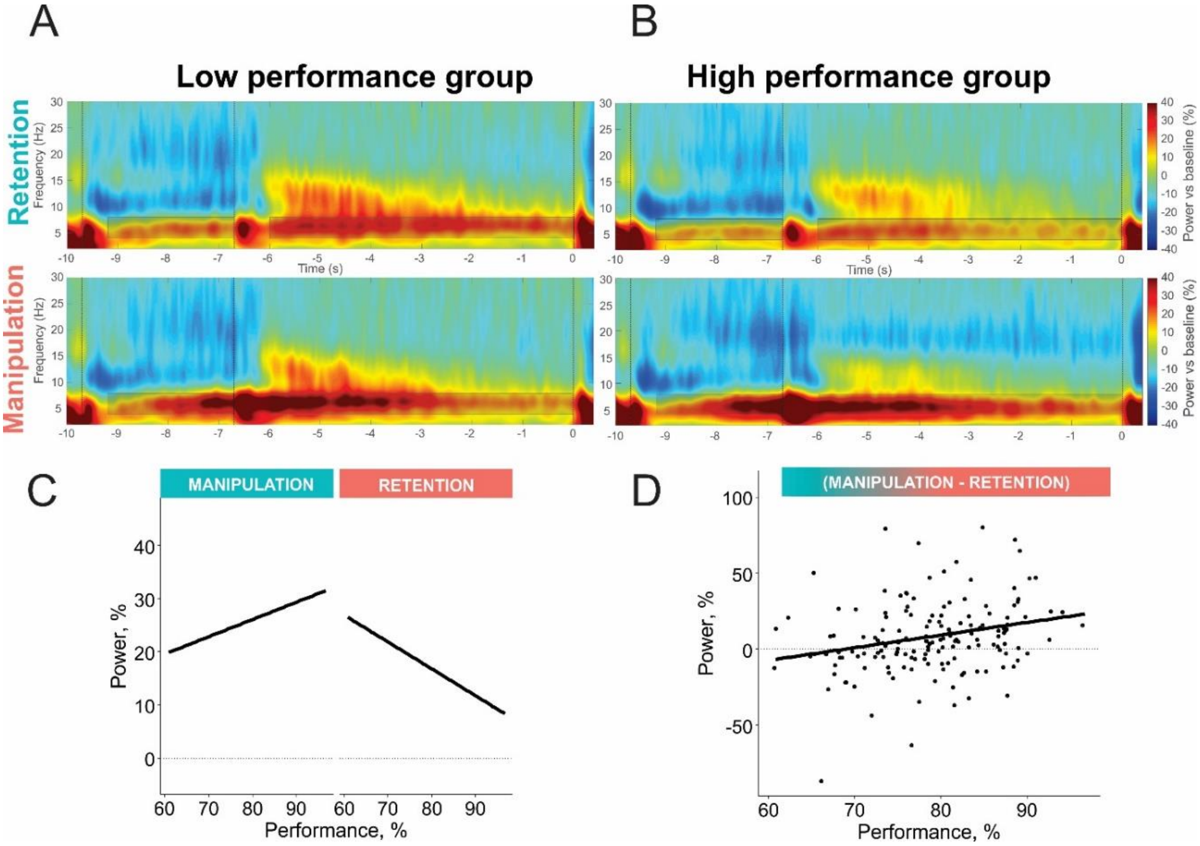

Figure 27 – Relationship between theta power in Fz and WM performance. (A) Time-frequency map in low performance group in retention (top panel) and manipulation (bottom panel) tasks. (B) Time-frequency map in high performance group in retention (top panel) and manipulation (bottom panel) tasks. Semi-transparent boxes in A, B mark time-frequency windows of interest (4-8 Hz, 2.5 s of encoding, 6 s of delay). The first vertical bar marks the onset of encoding; the second one marks the onset of delay; and the third one marks the onset of retrieval. (C) Correlation of WM performance in the manipulation and retention tasks. (D) Correlation of WM performance and the result of subtraction of theta relative power in the retention task from the power in the manipulation task.

3.3.3.2 Alpha

The final model that converged successfully:

*Power ~ Hemisphere * TimeInt * Task * Load * Performance + (Hemisphere+TimeInt+Load+Task+Task:Load+Task:Load:Hemisphere:TimeInt|Participant)*

As shown in Table 12 no significant main effects or interactions with Performance were found in the alpha frequency band.

Table 12 – Alpha LMM

	β	*SE*	*t*	*p*
(Intercept)	-0.051	0.017	-3.054	0.003
Performance	-0.020	0.017	-1.173	0.243
Hemisphere:Performance	0.009	0.005	1.924	0.056
TimeInt:Performance	0.004	0.014	0.310	0.757
Task:Performance	0.005	0.007	0.666	0.506
Load:Performance	0.005	0.007	0.678	0.499
Hemisphere:TimeInt:Performance	0.002	0.002	0.974	0.330
Hemisphere:Task:Performance	<0.001	0.002	0.072	0.943
TimeInt:Task:Performance	0.001	0.002	0.467	0.640
Hemisphere:Load:Performance	-0.002	0.002	-0.778	0.436
TimeInt:Load:Performance	0.001	0.003	0.367	0.714
Task:Load:Performance	0.015	0.008	1.884	0.061
Hemisphere:TimeInt:Task:Performance	-0.003	0.002	-1.294	0.196
Hemisphere:TimeInt:Load:Performance	0.002	0.003	0.632	0.527
Hemisphere:Task:Load:Performance	0.002	0.002	0.839	0.402
TimeInt:Task:Load:Performance	0.006	0.003	1.964	0.050
Hemisphere:TimeInt:Task:Load:Performance	0.002	0.003	0.578	0.564

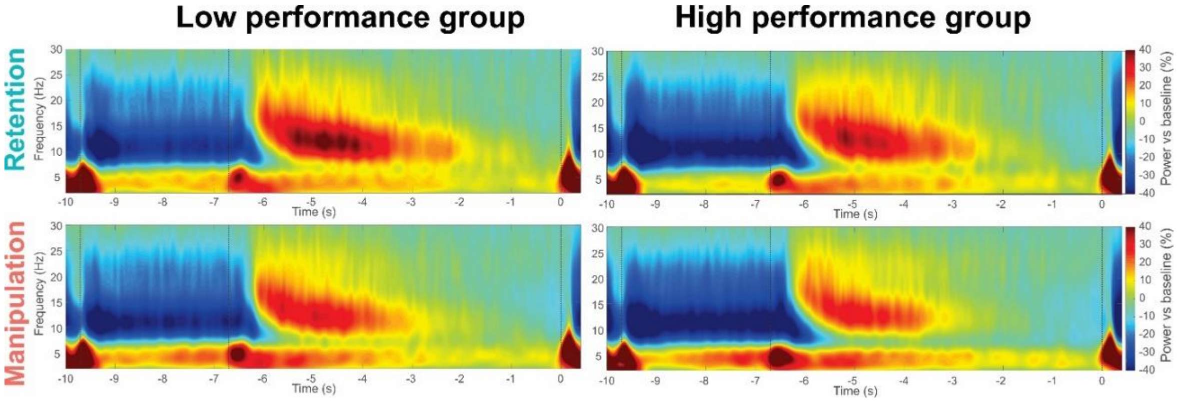

Figure 28 – Alpha spectral power and individual differences. Time-frequency map in low performance group in retention (top left panel) and manipulation (bottom left panel) tasks. Time-frequency map in high performance group in retention (top right panel) and manipulation (bottom right panel) tasks.

3.3.3.3 Beta

The maximal model successfully converged. In *lmer* syntax the final model can be described by the following formula:

*Power ~ TimeInt * Task * Load * Performance + (TimeInt*Load*Task |Participant)*

The LMM results in beta frequency band are shown in Table 13. The Task by Performance interaction indicates a negative relationship of beta power and WM performance in the Manipulation task but not in the Retention task (see Figure 29C). Like it has been done with the theta activity, a subtraction of Retention beta from Manipulation beta was taken as an index of executive WM components. The correlation between this index and WM performance had exactly the same magnitude as yielded in the analysis of theta (r = -0.24, p = 0.003), but with the opposite sign (see Figure 29D). Thus better performance was related to lower beta activity.

Table 13 – Beta LMM

	β	*SE*	*t*	*p*
(Intercept)	-13.38	0.75	-17.93	< 0.0001
Performance	-0.96	0.75	-1.29	0.200
TimeInt:Performance	-0.3	0.48	-0.63	0.533
Task:Performance	1.17	0.38	3.04	**0.003**
Load:Performance	-0.62	0.43	-1.46	0.147
TimeInt:Task:Performance	0.35	0.16	2.28	0.024
TimeInt:Load:Performance	-0.28	0.18	-1.59	0.113
Task:Load:Performance	0.45	0.43	1.06	0.292
TimeInt:Task:Load:Performance	0.03	0.18	0.17	0.868

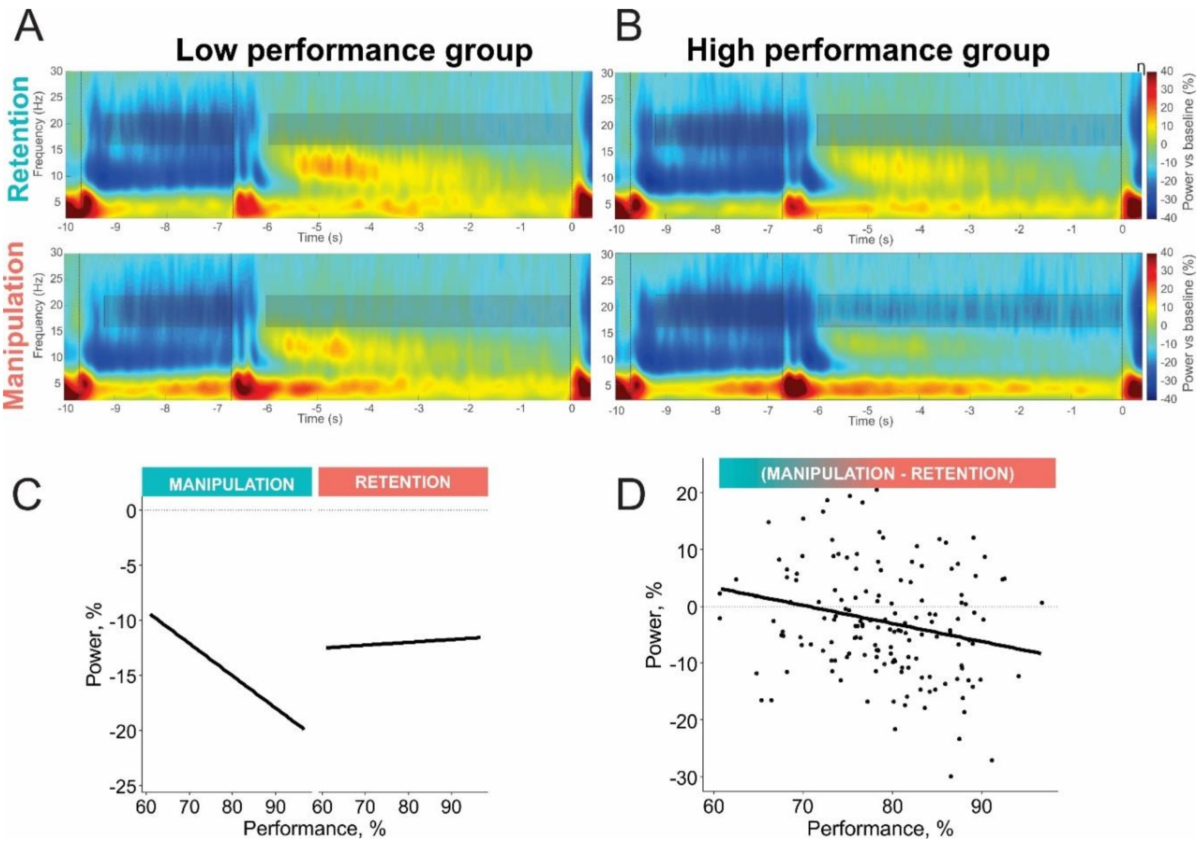

Figure 29 – Beta spectral power and individual differences. (A) Time-frequency map in low performance group in retention (top panel) and manipulation (bottom panel) tasks. (B) Time-frequency map in high performance group in retention (top panel) and manipulation (bottom panel) tasks. Semi-transparent boxes in A, B mark time-frequency windows of interest (16-22 Hz, 2.5 s of encoding, 6 s of delay). The first vertical bar marks the onset of encoding; the second bar marks the onset of delay; and the third one marks the onset of retrieval. Spectral power is averaged in Cz, C4, C3 channels. (C) Correlation of WM performance in the manipulation and retention tasks. (D) Correlation of WM performance and the result of subtraction of theta relative power in the retention task from the power in the manipulation task.

DISCUSSION

4.1 Load effects

The experimental manipulations with set-size produced an expected effect on accuracy. The accuracy decreased with an increasing WM load.

4.1.1 Event-related potentials

I did not have any hypotheses concerning the ERPs to the onset of the delay period. However, some statistically significant results were obtained. Particularly, the amplitude of P2 was larger in the most difficult 7-letters condition than in the other levels of load. In WM studies P2 has been interpreted as a representation of general arousal caused by cognitive stress. For example, expectation of the higher load condition enhanced the fixation cross P2 before presentation of the stimuli (Lenartowicz et al., 2014; Wolach & Pratt, 2001). If P2 critically depends on cognitive stress, it should be larger in the manipulation condition than in the retention condition. However, neither the main effect of Task nor the Load by Task interaction was found. A change in visual input and perceptual load might influence the amplitude of P2 (Crowley & Colrain, 2004). However, no difference was found in comparison of the lowest load level (5 letters) with the intermediate load level (6 letters). Nevertheless, an increase of perceptual load is the most plausible explanation of the effect.

The expected decrease of encoding P3 with an increasing load was not found. Load effects are not well represented in ERPs at higher levels of load. The saturation of encoding P3b at the 4 items level of load has been demonstrated (Grune et al., 1996; Scharinger et al., 2017). As was shown in a systematic review by Kotchoubey (2002), the most reproducible effect in WM ERPs is a significant difference between the lowest level of load (1 item) and all the others. The P3b amplitude was interpreted to represent resources dedicated to stimulus processing (Houlihan et al., 1998). In this study the stimulus was on the screen for a prolonged period of time and the WM items could be processed immediately but there was no high time pressure. When encoding is distributed over time, the amount of attentional resources dedicated to the task per time unit may not depend on of the set-size anymore. The information can be processed in smaller chunks without overloading the system.

Retrieval P3b was also expected to decrease with load but the opposite effect was obtained. The effect of retrieval attenuation with an increasing load is not always present in the literature. For example, in Kotchoubey et al. (1996) retrieval P3b decreased from 1 to 2 items but did not attenuate further. P3b to the probe was sometimes even reported to be larger in higher load conditions (Silva-Pereyra et al., 2001). Another study reported an increase of P3b with increasing load between 3 and 5 items (Ruchkin et al., 1992). In the study of Speer & Soldan (2015), P3b increased with load in the encoding phase but decreased in the retrieval phase. The exact dynamics of retrieval P3 can, therefore, strongly depend on the requirements of the task that remain to be investigated.

In the classic Sternberg task only correct recognition of the probe is required. In my version of the task the participants had not only to recognize the stimulus but also to identify its correct position. The memory search was probably happening twice: once to match the letter and second time to match the position. Moreover, the participants were not required to respond as fast as possible. In this condition they could take time and process the probe without overloading the memory storage. In this circumstances, P3b is a representation of attention rather than memory. The difference between RT and the latency of P3b was quite big. The average RT was about 2.5 seconds and the average P3b latency was about 500 ms. The latency of P3b is not different from earlier studies using the Sternberg task but RT is sufficiently delayed (for a systematic review see Verleger, 1997). For example, in Wolach & Pratt (2001) memorizing 4 items led to 490 ms latency of P3b, while the RT was 1099 ms. P3b, memory retrieval, memory search and decision making are rather disentangled in my case.

Larger amplitudes in more difficult conditions may reflect the motivational value of the probe to complete the task but not the direct retrieval of the memory content. Probably, the amount of effort dedicated to the task is also reflected in P3b amplitude. Thus, the hypothesis of general arousal and attention allocation is applicable to the later components such as P3b.

4.1.2 Slow cortical potentials

Considering the nature of the task with a relatively long delay period, I expected to use SCP as an appropriate measure of WM load in the time domain. The hypothesis was supported by the literature quantifying similar negativities in response to WM load (Luria et al., 2016; McEvoy et al., 1998; Ruchkin et al., 1990). First of all, it is important to distinguish the slow negativity found in my study from the other negativities observed in similar conditions. As was noticed earlier, the CNV in WM tasks typically decreases with load (i.e. it becomes more positive in higher load conditions) (McEvoy et al., 1998). SCP in my study clearly decreased in the more challenging manipulation task. This makes the SCP in my study unlikely to be a CNV. The similarity with CDA is also lacking, because the latter is a short-living phenomenon, whereas the present SCP lasted throughout the encoding and delay periods and never returned to the baseline. The present SCP were positive at posterior sites and negative at fronto-central sites, which is reminiscent to the SCP reported by Ruchkin et al. (1994, 1999, 1992, 1995, 1990) but completely different from the typical posterior-occipital distribution in CDA studies.

Furthermore, the SCP was strongly left lateralized. The left hemisphere lateralization was demonstrated earlier (e.g. Khader et al., 2007; Ruchkin et al., 1992), but not, for example, in the study of Mecklinger and Pfeifer (1996) who investigated both object and spatial WM tasks. They found largely fronto-central SCP in the object task but posterior SCP in the spatial task, which suggests spatial specificity of SCP. Verbal WM would involve activation of verbal cortical areas as reflected in left fronto-central SCP. In accordance with this, SCP was linked to rehearsal processes in WM and to the activity of the phonological loop (Ruchkin et al., 1990). However, a later work showed that articulatory suppression did not affect SCP (Murphy, Roodenrys, & Fox, 2006). Therefore, SCP during delay does not directly reflect verbal rehearsal. Nevertheless, the left frontal distribution revealed in the present study as well in Ruchkin et al. (1994, 1999, 1992, 1995, 1990) may suggest that SCP are related to maintenance of verbal information in WM.

Contrary to the expectations, no effect of load on SCP was found. Most of the evidence relating SCP and WM comes from Ruchkin et al. studies conducted in the 1990's. A more recent work found a saturation of SCP (termed negative slow wave by the authors) on the level of 3 items when compared with 5 items load condition (Liu et al., 2018). No one has ever compared SCP in a 5 items load condition with higher levels of load. A possible explanation of clearly above the chance level performance in 6 and 7 letters load and no changes in SCP are probably related to the hypothesis of “activity silent mechanisms” of WM (Kamiński & Rutishauser, 2019). I shall discuss this hypothesis in details below in Section 4.3.

4.1.3 Time-frequency analysis

Figure 30 presents a graphical summary of the findings reported in details in Section 3.2.3 in Results above. No clear load effect was obtained in any of the studied frequency bands.

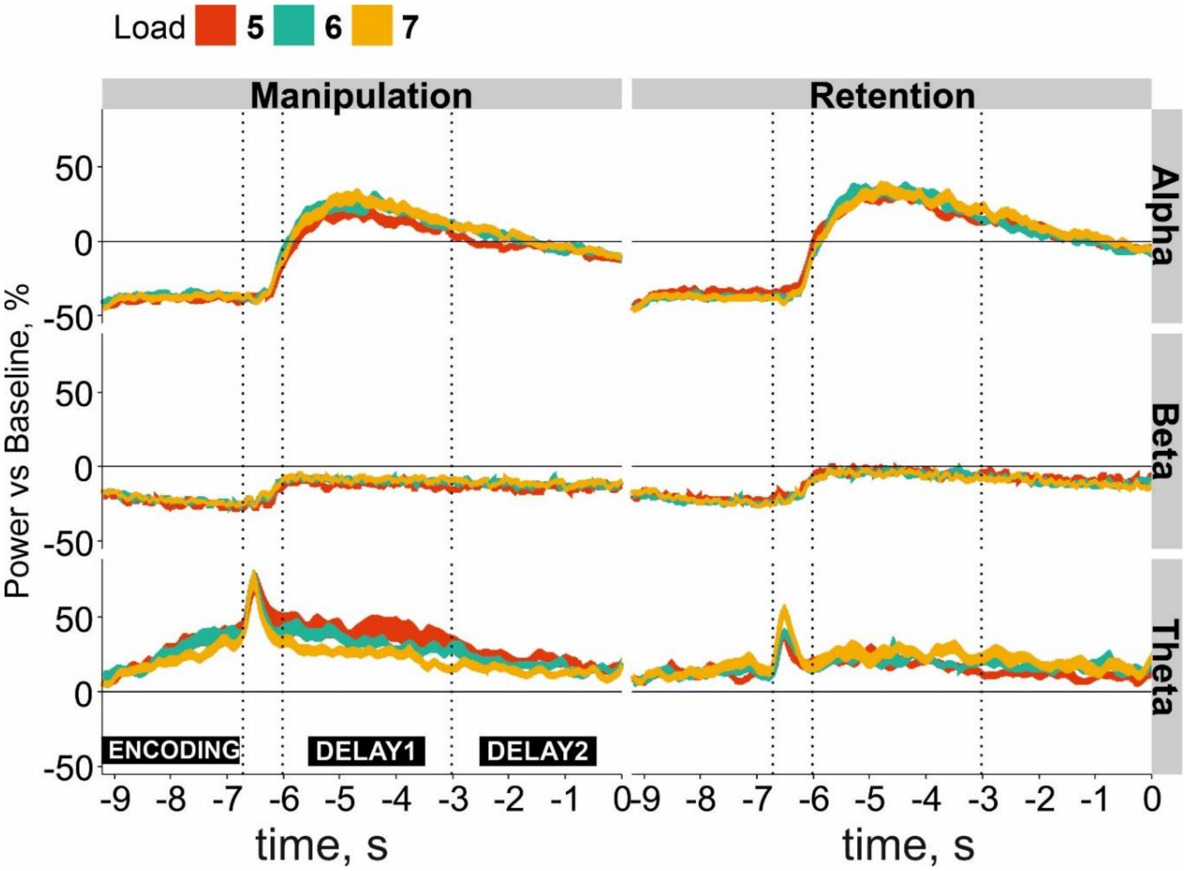

Figure 30 – Effects of Load in all studied frequency bands and conditions. Thickness of the lines represents mean ± SE.

4.1.3.1 Theta

As expected, the task demand led to an increase in theta activity in comparison with baseline. The role of theta activity in WM is hypothesized to be related to increasing demands for the maintenance of temporal relationship between items (Hsieh & Ranganath, 2014). In the present study the temporal order played a vital role in successful performance of the task. In previous studies this requirement led to enhanced theta activity (Hsieh et al., 2011; Roberts et al., 2013). In the current study the effect of increased theta during delay was extremely strong (one-sample $t(155) = 8.88$, $p < 0.0001$, Cohen's $d = 0.71$). The theta enhancement correlating with memory performance is another piece of evidence to confirm the importance of FMT in WM.

According to Hsieh & Ranganath (2014) the increase of the set-size would also increase the complexity of the temporal order relationships between the memory items. Therefore, not only the requirement of manipulation but also increasing memory load should result in theta enhancement during delay. However, no load-dependent effect was found. As was demonstrated in the systematic review in the introduction, theta increase with increasing WM load was found in some studies but not in all of them. A load dependent increase in a visual WM task saturated at 4 items in one study (Zhang, Zhao, Bai, & Tian, 2016). A verbal MEG study found FMT increase from 2- to 5- but saturation in the 8-letters maintenance condition (Brookes et al., 2011). Because my experiments used 5 to 7 items sets, FMT could have been at a plateau. Although my data (along with the data of the systematic review) support the significance of theta oscillations in WM performance, Hsieh & Ranganath's (2014) hypothesis is not supported regarding the role of memory load. The role of theta activity in the coordination of information stored in the cortical regions maintaining information in WM is stressed by a number of authors (Raghavachari et al., 2001; Sauseng et al., 2010). This topic is further discussed below in section 4.2.3.1.

4.1.3.2 Alpha

Alpha activity showed a pattern of suppression during encoding which was reversed during delay. A similar alpha time course has been observed in previous studies. A group of researchers demonstrated independently in different samples a pattern of alpha suppression during encoding that switched to a continuous enhancement starting from 1 s after the onset of the delay (Embury et al., 2018, 2019; Heinrichs-Graham & Wilson, 2015; McDermott et al., 2016; Proskovec et al., 2016; Wiesman et al., 2016; Wilson et al., 2017). Heinrichs-Graham & Wilson (2015) suggested that at later stages of WM tasks the alpha activity is required to counteract forgetting. This hypothesis, however, is not supported by the present data demonstrating that at the end of a long delay period, alpha returns to the baseline level despite the increasing likelihood of forgetting with time. In all previously mentioned studies this phenomenon could not be found because the delay was only 3 s long.

Shifts of attention are hypothesized to be related with the directionality of alpha changes (Wianda & Ross, 2019). When attention is directed to the external information, alpha suppression indicates an active state of visual information processing. This effect is related to increased performance in perceptual tasks (Hanslmayr et al., 2007; van Dijk, Schoffelen, Oostenveld, & Jensen, 2008). Subsequent alpha synchronization was attributed to the inhibition of visual input to protect memory from interference (Bonnefond & Jensen, 2012; Wianda & Ross, 2019). As was demonstrated in the systematic review, alpha does not always increase with the onset of delay. Nevertheless, linking alpha enhancement to the interference prevention function may serve as a possible explanation.

A large body of the literature suggests that internal attention modulates alpha on a large scale (de Vries, van Driel, Karacaoglu, & Olivers, 2018; Fukuda et al., 2015; Schneider, Goddertz, Haase, Hickey, & Wascher, 2019). In WM research previously presented spatial cues may direct internal attention and affect alpha activity. For example, when internal attention is directed to the left hemifield items maintained in memory, right posterior alpha activity is attenuated (de Vries et al., 2018; Myers, Walther, Wallis, Stokes, & Nobre, 2015; Sauseng et al., 2009; Wolff, Jochim, Akyürek, & Stokes, 2017; Worden, Foxe, Wang, & Simpson, 2000). Furthermore, when transcranial magnetic stimulation at 10 Hz was delivered to the ipsilateral hemisphere, i.e., to the area processing irrelevant information, then behavioral performance was increased. Application of the same type of stimulation to the cortical area maintaining relevant information hindered WM (Sauseng et al., 2009). Existing evidence suggests that an alpha increase during maintenance reflects sensory gating through the disengagement of certain cortical areas to protect memory representations from interference (Klimesch et al., 2007; Payne & Sekuler, 2014; Roux & Uhlhaas, 2014). From this perspective alpha suppression is a sign of cortical engagement (Jensen & Mazaheri, 2010) allowing either encoding of information into WM or decoding the information for retrieval (Klimesch et al., 2007). Thus, alpha suppression during encoding probably reflects the active state of visual information processing. The alpha enhancement at the start of the delay signalizes switching to the state of inhibition of the visual input.

In my study the effect of alpha synchronization during delay was prominently right side lateralized. The effect cannot be explained by asymmetric stimulation. All the stimuli were presented in the middle of the screen with no lateralization and no spatial cues. Right hemisphere alpha increase is not uncommon in verbal WM tasks. The results of the systematic review demonstrate a prevalence of right-lateralized alpha in verbal WM tasks as measured by EEG (see Table 14). In the EEG studies where topographical maps were reported, alpha synchronization effect had right asymmetry in 10 studies, no asymmetry in 3, and no studies reported left hemisphere alpha synchronization during delay. Verbal WM MEG studies confirm stronger alpha synchronization in the right occipital areas during delay period (Kustermann, Popov, et al., 2018; Kustermann, Rockstroh, et al., 2018; McDermott et al., 2016; Wianda & Ross, 2019).

The mainstream interpretation of alpha synchronization during delay is the suppression of task-irrelevant regions (Bonnefond & Jensen, 2012; Jensen & Mazaheri, 2010). But why the activity of the right temporo-parieto-occipital region during a WM task performance should be irrelevant? This region has been found to be associated with the processing and storage of visuo-spatial information (Berger et al., 2019; Linden, 2007; Rahm, Kaiser, Unterrainer, Simon, & Bledowski, 2014). However, a few visual studies demonstrated a significant asymmetry effect with more synchronized alpha over the right occipital area (Johnson et al., 2011; Mapelli & Ozkurt, 2019; Maurer et al., 2015). Mapelli & Ozkurt et al. explain the effect of stronger alpha desynchronization in the left hemisphere by the role of the left cortex in the binding of perceptual features. The alpha desynchronization revealed in my data most likely signalizes the importance of the left hemisphere in maintenance of verbal information. This hypothesis is also supported by the effect of stronger alpha suppression in the manipulation task that was found only in the left hemisphere (further discussed in Section 4.2.3.2).

Table 14 – Alpha asymmetry in the verbal WM studies featuring alpha activity in the results. Only the studies reviewed in the systematic review included to the table.

Reference	***Alpha lateralization***
Bashivan et al., 2014	right
Berger et al., 2014	-
Chou et al., 2015	-
Fingelkurts et al., 2002	right
Harmony et al., 1996	-
Hwang et al., 2005	symmetry
Itthipuripat, Wessel, & Aron, 2013	-
Jensen et al., 2002	right
Kawasaki, Kitajo, & Yamaguchi, 2010	-
Khader et al., 2010	symmetry
Klimesch et al., 1999	right
Kwon et al., 2015	-
Melnik, Mapelli, & Ozkurt, 2017	right
Meltzer et al., 2007	symmetry
Michels et al., 2008	-
Michels et al., 2010	right
Okuhata, Kusanagi, & Kobayashi, 2013	-
Pavlov & Kotchoubey, 2017	right
Schack & Klimesch, 2002	-
Scheeringa et al., 2009	right
Stokic et al., 2015	right
Wilson, Swain, & Ullsperger, 1999	right

Notes: - – no information is available, right – stronger alpha power/synchronization in the right hemisphere, symmetry – no clear difference between the hemispheres

In my study alpha depended on WM load neither during encoding nor during delay. Like in the case of theta, this might be explained by the alpha activity being already at a plateau with the lowest load of 5 items. Similar findings of no load-dependent alpha change above 5 items were reported in the literature (Bashivan et al., 2014; Scheeringa et al., 2009; Stokic et al., 2015). I will further discuss the role of alpha activity in Section 4.3.

4.1.3.3 Beta

Generally, beta activity (16-22 Hz) was desynchronized throughout the task performance. No effect of Load was statistically significant. The possible meaning of beta oscillations in verbal WM is thoroughly discussed in the next section dedicated to the effects of Task.

4.2 Components of WM

A core feature of the WM construct is the requirement to maintain and manipulate information simultaneously (Oberauer, Süß, Schulze, Wilhelm, & Wittmann, 2000). In the present study these two key elements of WM were separated from each other. The retention task involved only maintenance of the originally presented set of items. In addition to that, in the manipulation task the participants were required to conduct several other subtasks. First, the task involved an access to the alphabet in the long-term memory. Next, the task required reordering the letters to match the template in the long-term memory, while maintaining the original set. When the reordering was finished, not only did the newly formed set had to be maintained in WM, but also the original set had to be suppressed. In addition to the listed operations, switching between the original and reorganized set was involved. The task required distribution of attentional resources, in fact multitasking. As a result, the RT was longer and the accuracy was lower in the manipulation as compared to the retention task.

4.2.1 Event-related potentials

The effect of Task in P3b time window was observed in response to the onset of both encoding and retrieval. However, the direction of the effect was different in different stages of stimulus processing. Encoding P3b was larger in the retention task and retrieval P3b was larger in the manipulation task.

Seemingly, the identical amount of information should be encoded in both Manipulation and Retention tasks. Nevertheless, in the manipulation task the additional requirement to rearrange letters created a situation of multitasking. It is further possible that some subjects tried to start the reordering already at the encoding stage. The situation of distributed attention between two tasks could lead to a decrease of encoding P3. Though the literature on encoding P3 is scarce, generally, the relationship between attentional demands and amplitude of P3 is a phenomenon observed in multiple occasions (Kok, 2001; Kotchoubey, 2002; Watter et al., 2001). In the present design, since participants already know the task from the beginning of a trial, at the presentation of stimuli they can already have built a set “it will be difficult” or “it will be not very difficult”. The anticipation of a difficult task, together with the corresponding distraction of attention toward the process of reordering, might be the reason for the decrease of encoding P3b.

The differences between ERPs in WM and STM tasks are not well represented in the literature, perhaps, because ERPs in the range of one second after stimulus onset are not sensitive enough to long-term processes such as manipulation of information in WM. To the best of my knowledge, there is only one work that compared ERPs in manipulation and simple retention tasks in all three phases: encoding, delay and retrieval. In this visual WM study a similar decrease of encoding P3a and P3b amplitudes in the manipulation task was found (Román-López et al., 2019). The dual-task nature of the manipulation task can be responsible for the division of attention leading to the observed decrease in the amplitude. Similarly, in the letters rotation task, the larger was the angle of the rotation, the stronger was the attenuation of P3b (Ma et al., 2016; Wang et al., 2017; Wijers, Otten, Feenstra, Mulder, & Mulder, 1989).

Further in the course of the task performance, the retrieval phase reversed the relationship between the P3 amplitude and task requirements. A larger P3 was found in the manipulation condition. Román-López et al. (2019) also showed a larger retrieval P3b in the manipulation task. Like in my results, the effect was better pronounced at frontal sites. P3b in response to the probe was larger after backward manipulation than after simple retention task (Liu, Zhou, Wang, Jiang, & Liu, 2017). In another backward recall task the opposite relationship between P3 amplitude and the type of the task was found (Nulsen, Fox, & Hammond, 2010). Probably, the most noticeable difference between the two studies was the duration of time window when the response could be given. In Nulsen et al.’s study the response had to be given immediately because items were presented in fast succession. In Liu et al.’s study the probe was followed by a long response window. Similarly, in my study there was no time pressure to make a response, resulting in perceptual processing, decision making and reaction to the probe being disentangled. For this reason, the effect of increased P3b is rather a reflection of the motivational value or the onset of memory search, but not a manifestation of the search. In other words, P3b is not the final stage of task performance but a pure reaction to the probe itself.

4.2.2 Slow cortical potentials

SCP were more negative in the manipulation task than in the retention one. It has been suggested that SCP are related to the functioning of the phonological loop and hence reflect rehearsal processes. If the hypothesis is true, then a left frontal spatial distribution would be expected. At first glance, it might appear as a contradiction that the effect was localized in the midline channels and did not differentiate between time intervals. No interaction with the hemisphere was found as well. However, the contradiction can be removed if rehearsal processes in the manipulation task do not differ very much from those in simple retention. This is even more plausible if we assume that rehearsal is still possible in parallel with verbalization (Camos & Barrouillet, 2014). This possibility may explain the lack of regional specificity.

If the phonological loop is not the source of the observed effect, then, probably, SCP amplitude may be a function of the consumption of attentional resources. Similar effects were demonstrated in previous studies (Liu, Guo, & Luo, 2010; Monfort & Pouthas, 2003; Román-López et al., 2019). Thus, manipulation caused larger SCP during delay than retention in visual WM tasks (Liu et al., 2010; Román-López et al., 2019). Moreover, midline localization of the effect suggests that SCP can partially be explained by anticipatory and preparatory mechanisms in expectation of the probe. On the one hand, CNV is attenuated with higher cognitive load (Gevins et al., 1996; McEvoy et al., 1998). On the other hand, CNV might have been increased because the probes in the manipulation task have a higher motivational value. Therefore, the observed effect is probably a combination of the SCP representing larger general energy consumption and the CNV in anticipation of a more challenging probe.

4.2.3 Time-frequency analysis

A visual summary of the obtained effects is depicted in Figure 31.

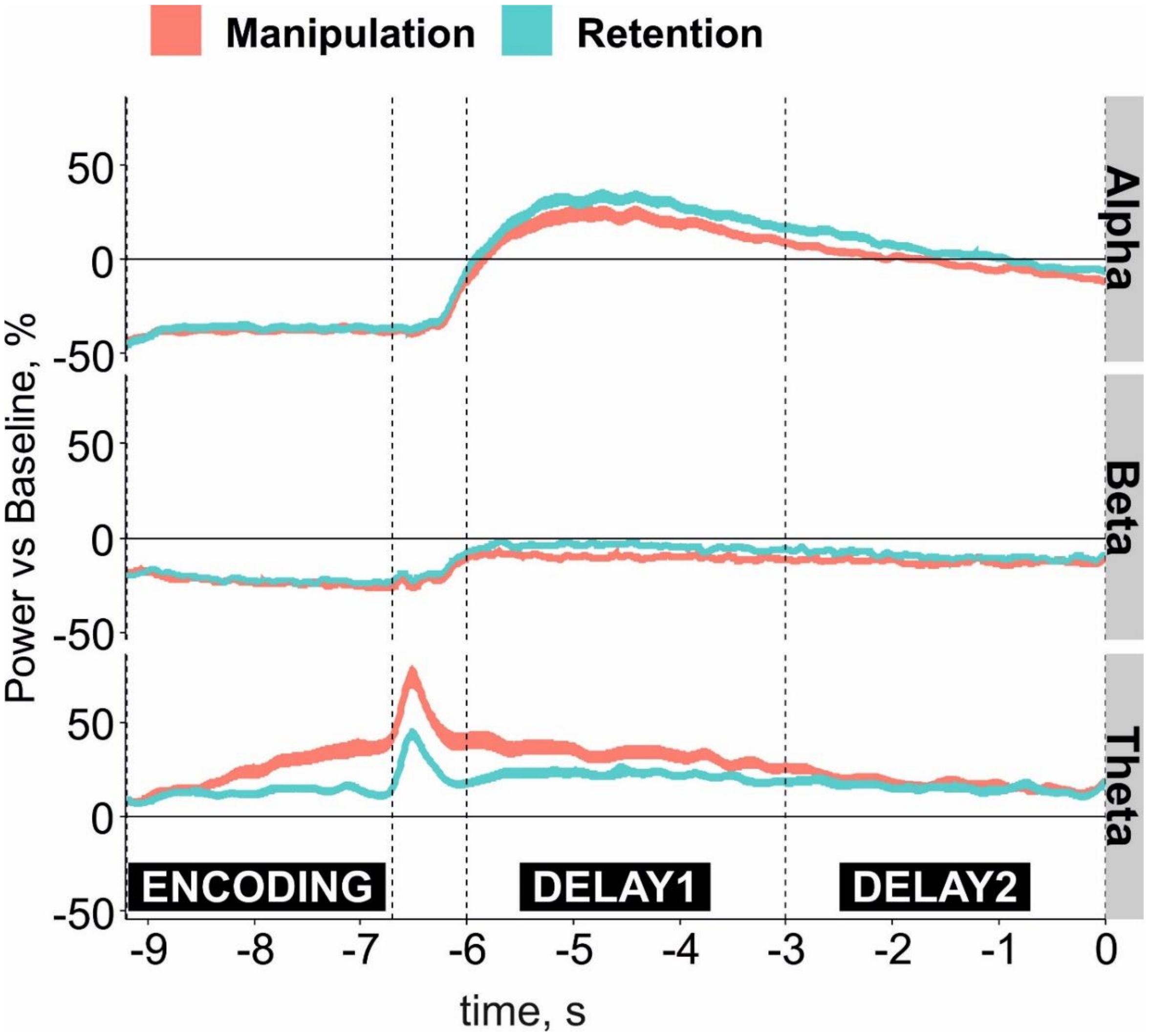

Figure 31 – Spectral power in theta, alpha and beta frequency bands over time. Thickness of the line is defined as mean ± SEM.

4.2.3.1 Theta

Theta activity was greater in the manipulation as compared to the retention task. The close relationship between manipulations in verbal WM and theta rhythm enhancement has been repeatedly observed in the literature (see the systematic review; see also a recent study by Román-López et al., 2019). Although in a recent spatial WM study by Berger et al. (2019) theta activity did not differ between the manipulation and retention tasks, it did in three other studies using the same experimental paradigm (Berger et al., 2016; Eschmann et al., 2018; Griesmayr et al., 2014). Increased theta fronto-parietal functional connectivity in the manipulation vs retention contrast confirmed the critical role of theta rhythm in successful performance of WM as opposed to STM tasks (Sauseng, Klimesch, Schabus, &

Doppelmayr, 2005). Despite minor inconsistencies in the findings, theta synchronization in the manipulation tasks is a well-replicated phenomenon at least in the verbal domain. My work confirms the role of theta activity in the control of attention and its relationship with the executive components of WM.

The difference between the conditions in the power of the theta frequency band was not stable in time (see Figure 31, theta panel). Theta started differentiating between the tasks at about 1 s in the encoding period and the difference disappeared at around 4 s in the delay period. This temporal profile may reflect the trajectory of the alphabetizing process. (Some) participants probably started manipulations while the stimuli were still on the screen and continued the task until it is completed – as expected, in the middle of the delay period. This finding is another important piece of evidence confirming that theta synchronization is a reflection of the increased demand on executive control network caused by the requirement of the task.

One might argue that the manipulation task was simply more demanding. From this point of view, not the increased involvement of the executive control networks but a general task difficulty (i.e., the required effort) produced the theta effect. However, the most obvious measure of task difficulty is the performance. The performance, as measured by the accuracy, was similar in 5A and 7R conditions. Nevertheless, the difference in theta spectral power between these two conditions was still substantial (main effect of Condition: $F(1, 155) = 10.55$, $p = 0.0014$, $\eta^2 = 0.06$). This result provides additional evidence that FMT is a marker of executive components of WM.

4.2.3.2 Alpha

On average, alpha returned to the baseline level by the beginning of the second part of delay. Nevertheless, the results showed that the effect of stronger alpha suppression in the manipulation task was present throughout the whole delay period. The difference between the tasks was not present during encoding. Assuming that manipulations could start before the onset of delay and end some time before the end of delay, mapping alpha activity on the manipulations performance is not justified.

Alpha suppression is hypothesized to reflect sensory information processing (Jensen & Mazaheri, 2010). The requirement of the task was to recombine letters into alphabetical order. The decrease of alpha during delay in the manipulation task suggests less strong inhibition of cortical areas actively involved in the processing of the information. It means that information encoding is not finished by the beginning of the delay period but continues. But it is not a sufficient explanation because the difference between manipulation and retention was observed even at the end of the delay when all encoding is expected to come to an end.

Alpha suppression can be seen as a sign of unspecific cortical activation during cognitively demanding mental processes (Berger et al., 2014; Sauseng, Klimesch, Doppelmayr, et al., 2005). The effect of stronger alpha suppression in the manipulation than in the retention task was present only in the left hemisphere, possibly indicating involvement of the language cortex into task processing. One might object against this hypothesis, that this involvement should also be manifested in an effect of WM load, but, as already said, this effect was not found. However, it is plausible that the difference (in terms of engagement of the language cortex) between the levels of load at the rather high range from 5 to 7 items is much subtler than the difference between the types of the task.

4.2.3.3 Beta

Unlike theta and alpha, beta activity was inhibited throughout the task as compared with baseline. In the first part of the delay period beta was more strongly suppressed in the manipulation than in the retention condition. The functional role of beta oscillations in WM is not well understood. Nevertheless, the effect is in line with the only available verbal WM study comparing the components of WM (Berger et al., 2014). Berger et al. found support for the status quo model of beta activity that asserts that beta oscillations are related to the maintenance of the current cognitive state (Engel and Fries, (2010). According to the model, when no changes in the cognitive state appears, beta is high, and as soon as new information processing is required, beta is suppressed. Updating and manipulating information in WM would change the current state of memory thus suppressing beta activity. The manipulation task required constant attention switching between the modified reordered string of letters and the original one. Above we already hypothesized that the reorganization of memory should be finished to the second half of the delay period, which can be regarded as the establishment of a stable “status quo”. This is exactly the time when the difference in beta activity between manipulation and retention disappeared. This finding speaks in support of the status quo model.

Against the status quo model, however, speaks the fact that the average power of beta in the second part of delay was lower than in the first part of it, while the model predicts the opposite relation. However, the beta suppression in the second part of the delay can be explained by preparation of the motor response. Similar beta activity between 15-20 Hz was observed by Proskovec, Heinrichs-Graham, et al. (2019) in the Sternberg task. Their beta appeared about 800 ms before the probe. Preparation to the following motor response might lead to such an activation. However, response preparation alone is not a satisfactory explanation for the beta effects obtained in the current experiment, because the effect of task in beta frequency band was significant only in the first part of the delay when no motor preparation is meaningful. Furthermore, motor preparation during encoding cannot explain even larger beta suppression than during delay period.

Another thinkable explanation might be that the motor cortex is involved not only in motor preparation but also in unintentional imaginary movements. The mental manipulations with the letters in WM involve a replacement of imaginary objects. This operation may engage motor areas. This hypothesis is, however, not supported by fMRI studies that did not find any involvement of premotor areas in WM manipulation tasks (D'Esposito et al., 1999; D'Esposito, Postle, & Rypma, 2000).

Other mechanisms may also yield beta changes during the mental manipulations. Although attention shifts from one object to another can occur without eye movements, the shifts activate the same cortical areas as real eye movements (Grosbras & Paus, 2002). A good example is the activation of frontal eye fields (FEF) found in a spatial manipulation task (Glahn et al., 2002). In the same study the DLPFC, the VLPFC, the posterior parietal lobe and the ACC were activated as well. These brain regions are also actively involved in WM tasks. FEF are a part of dorsal attention network heavily involved in the process of encoding of information to WM (Kim, 2019). Although there is no direct evidence of relationship between activation of frontal eye field and beta activity suppression, it may stand as a possible explanation.

To sum up, three possible factors may determine the dynamics of beta oscillations: the involvement of premotor cortical areas during mental manipulations, the maintenance of status quo (Engel & Fries, 2010) after finishing the manipulations, and response preparation at the end of the delay interval.

4.3 Duration of delay

A long delay period was employed to investigate the effect of duration of the delay period on the oscillatory brain activity. The analysis included a comparison of the first and the second parts of the delay. The effect was strong in all studied frequency bands. The results of the corresponding analyses were described above in Section 3.2.3 and are summarized here in Figure 32.

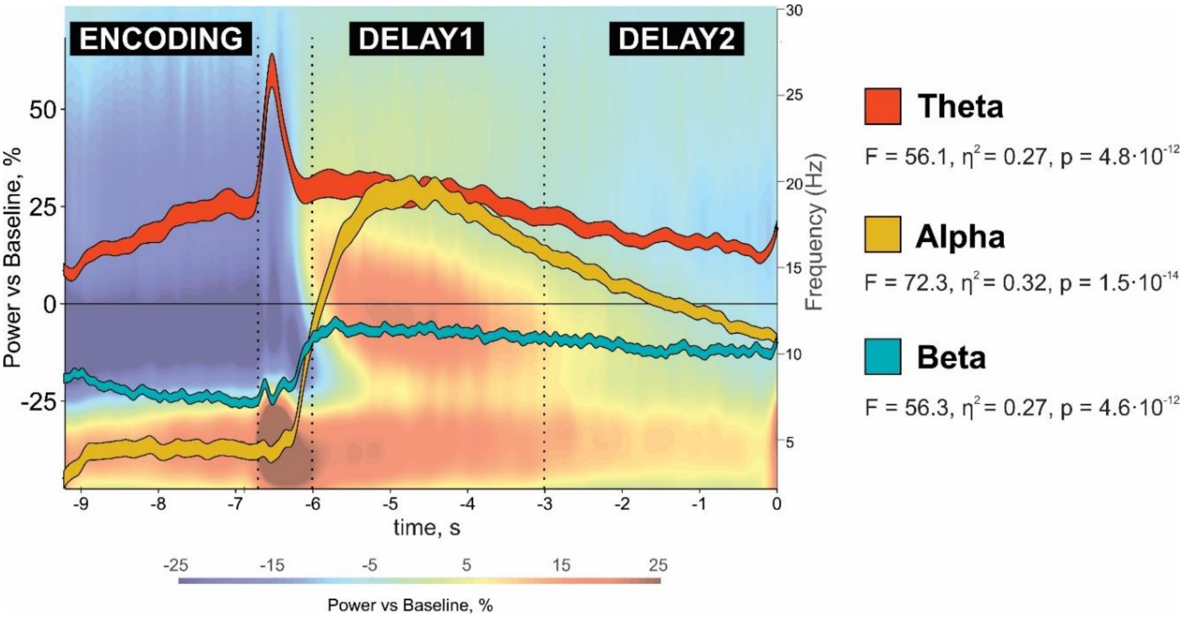

Figure 32 – Time effects (comparison of Delay1 and Delay2 time intervals). The temporal dynamics of the frequencies and the statistical output of the ANOVA RM with a 2-level factor Time interval are shown. The thickness of the lines represents standard error of the mean. Time-frequency map is the grand average at the posterior, central and Fz electrodes.

There is no evidence of verbal WM performance decline with increased duration of the delay when no concurrent task is presented (Oberauer et al., 2016, 2018). Therefore, one would expect to observe constant neural activity throughout the delay period. This idea is also supported by the view that the essence of WM is the sustaining neural firing (Constantinidis et al., 2018). This expectation was not confirmed in my study. As was noted in the systematic review, only few M/EEG studies employed experimental paradigms with delays longer than 4 s. Ellmore et al. (2017) is the only available WM study with a long enough delay (6 s) that reports TF representations of alpha activity and formal statistical analysis of the time effect. The authors demonstrated that alpha behavior during delay was transient rather than sustained. In the current study no sustained activity in any frequency band was observed. Moreover, alpha activity, commonly related to information maintained in memory (Foster, Sutterer, Serences, Vogel, & Awh, 2016; Sutterer, Foster, Adam, Vogel, & Awh, 2019; Wianda & Ross, 2019), disappeared in the second part of the delay.

There is mounting evidence that information in WM can be maintained without detectable neural activity related to the maintained information. Strong support for this idea comes from machine learning studies aiming to decode the content of WM from EEG and fMRI data (Bae & Luck, 2018; Lewis-Peacock, Drysdale, Oberauer, & Postle, 2011; Rose et al., 2016; Wolff et al., 2017). The studies showed the possibility to match neural patterns with specific content currently maintained in WM. However, the decodability quickly disappeared, which led to a hypothesis that neural activity may represent not the entire content but only information in the focus of attention (Lewis-Peacock et al., 2011; Stokes, 2015; Wolff, Ding, Myers, & Stokes, 2015; Wolff et al., 2017).

For example, Wolff et al. (2017) used lateralized alpha-activity in the retro-cue paradigm as a read-out of WM content. In this paradigm, participants had to encode two items located on both sides of the fixation point. A retro-cue, presented after a short delay, informed the participants which item should be kept in memory and which item is no longer relevant. The alpha activity demonstrates a lateralized pattern being stronger suppressed over the hemisphere contralateral to the cued item. The authors were able to decode above the chance level the content of WM until the end of the delay. However, the figures show that decoding accuracy quickly deteriorated and even approached the chance level towards the end of delay (<1 s).

In another study employing the same approach the accuracy of the classification declined below chance level shortly before the end of the delay, i.e., 700 ms after the delay onset (Wolff, Kandemir, Stokes, & Akyürek, 2019). It was possible to decode only the attended item. The unattended information quickly lost its ability to be decoded.

Nevertheless, all the information was remembered after the delay ended. The information that is still available for retrieval but not detectable through correlates of neural activity was termed as activity-silent (Stokes, 2015).

The inability to decode information from such a noisy signal as EEG provides some evidence for the activity-silent model of WM but it may be related to the limitations of the method. The data of intracranial recordings support the notion that the inability to detect WM content in EEG is not related to the limitations of the recording technique. In monkeys, the neural activity related to WM maintenance can completely disappear during the delay returning only shortly before the probe when a decision has to be made (Barak, Tsodyks, & Romo, 2010). Typical WM experiments in monkeys use only one item for encoding. In an exceptional study employing a Sternberg type multi-item visual WM task (Konecky, Smith, & Olson, 2017), only the last item was represented by persistent firing while the other items were activity-silent. The activity-silent model of WM suggests that rapid changes in synaptic weights allow to maintain information in WM even in the absence of persistent neural activity (Manohar, Zokaei, Fallon, Vogels, & Husain, 2019; Silvanto, 2017; Stokes, 2015). Probably, persistent activity maintains the memory when the remembered item is in the active state of focused attention. When attention is shifted to another item, WM is stored in activity-silent synaptic traces.

An alternative model postulates a separation of the processes taking place during the WM delay period into iconic, transient and sustained stores (Ruchkin, Grafman, Cameron, & Berndt, 2003). The stores are characterized by timing of the activation. The transient store in the model operates over about 4 s after the onset of the delay. The role of the transient store is to translate information from iconic into a more sustained long-term form. Following this view, the actual duration of what we call WM or STM is about 4-5 seconds long, after which LTM begins. Corroborating the idea, performance in WM shows a similar deficit after about 5 s like in LTM tasks in patients with medial temporal lobe lesions (Jeneson & Squire, 2011). The first 4 s may represent a sensitive period of memory consolidation. Ranganath et al. (2005) showed that presentation of a visual distractor after 1 s of delay disturbed LTM performance, whereas a presentation of the distractor 4 s after the delay onset did not affect later recall. These findings suggest that WM after 4 s delay is not so different from LTM.

I observed neither persistent neural delay activity nor completely activity-silent delay. Rather, the activity was strongly different in the first and the second part of the delay period. Apparently, delay activity is not a unitary phenomenon. For example, on average no alpha activity was present after about 4 sec of the delay. I hypothesize that the resulting pattern may be determined by an interplay of two mechanisms. At the beginning, neural firing is the leading mechanism supporting memory trace. As the time passes, the weight of this mechanism decreases, and another mechanism of rapid plasticity becomes more important. Perhaps, the latter mechanism fully takes over the responsibility of maintaining information in WM after 4 seconds of delay. At present this hypothesis remains speculative, and more research is needed to test it.

4.4 Individual differences

4.4.1 Theta

According to what has been said above, the difference between the relative spectral power in the retention and the manipulation conditions may be regarded as an EEG index of the executive components of WM. This index positively correlated with WM performance. Likewise, behavioral research showed that individual differences in executive functions were better predictors of WM capacity than differences in sensory storage (Engle, 2002; Shipstead et al., 2014; Unsworth & Spillers, 2010). Neuroimaging studies relating executive components of WM and neural underpinnings of individual differences are lacking. The only exclusion is the study by Hsieh (2011) with only 10 subjects per group, which strongly decreases the reliability of the conclusions drawn from this study. In the current work for the first time I demonstrated that electrophysiological correlates of executive control are significantly related to the behavioral performance in a WM task.

Despite the fact that in STM tasks the demand on executive functions is considerably lower than in genuine WM tasks, it is not completely lacking. For example, when WM load is high, executive components of WM are needed to counteract interference and to suppress irrelevant information. A few studies demonstrated a correlation between theta activity and performance in verbal (Zakrzewska & Brzezicka (2014): N=69, r=0.32, Kwon et al. (2015): N=13, r=0.76) and visual (Kawasaki & Yamaguchi (2013):

N=14, r=0.51; Maurer et al. (2015): N=24, r=-0.41) STM tasks. In contrast, I found no correlation between theta activity in the STM (Retention) task and behavioral performance (r = -0.03 for correlation with overall performance, r = -0.02 for correlation with performance in the retention task only). Similarly, Pahor & Jausovec (2017) failed to identify any differences in terms of theta power between high- and low-performance groups (N=30 in each group). In that study, however, the employment of the visual change detection task (Luck & Vogel, 1997) with a short delay (1 s) complicates generalization of the conclusions. In general, there are too many methodological differences among the above mentioned studies. For example, behavioral performance was measured as either average accuracy, or the difference in accuracy between the simplest and the most difficult conditions, or step-wise increment in accuracy. The measures of WM performance correlated with either relative or absolute theta power, or the difference in theta power between extreme levels of load. No single approach can unify all studies reviewed in this section.

Although Pahor & Jausovec (2017) did not find a correlation between theta power and WM performance, they reported increased theta fronto-parietal connectivity in the high-performance group. Also in the Simon task the high-performance group had the increased theta fronto-parietal connectivity (Gulbinaite, van Rijn, & Cohen, 2014). The Simon task is a common measure of executive control abilities although the correlation with WM performance is weak (Gulbinaite, van Rijn, & Cohen, 2014). The results above are suggestive to the role of theta in the coordination of information within a fronto-parietal network. More importantly, in addition to the general function of theta in the coordination, its effectiveness is able to modulate behavioral performance.

Fronto-parietal network activity has been linked to WM in other studies (D'Esposito & Postle, 2015; Palva, Monto, Kulashekhar, & Palva, 2010). The frontal node of the network is frequently associated with DLPFC activity (D'Esposito & Postle, 2015). As was noted in the introduction, DLPFC activation is the most reliable correlate of FMT. The DLPFC activity, as measured by fMRI-BOLD signal, increased in the WM task with manipulations (D'Esposito et al., 1999). Moreover, Postle et al. (2006) found that rTMS to the DLPFC disrupted performance in the manipulation task but not in the retention task. In two other rTMS studies the authors employed a Delayed-Response Alphabetization Task, which is quite similar to the task used in my study (Beynel et al., 2018; Beynel, Davis, Crowell, Hilbig, et al., 2019). They targeted the DLPFC with the same type of stimulation as Postle et al. (2006) (5Hz rTMS) in order to excite (not to inhibit) this area and thereby to improve WM performance. No reliable effect of rTMS on WM was demonstrated. The authors' initial hypothesis was puzzling because in a meta-analysis the same authors convincingly demonstrated that rTMS either has no effect (with stimulation frequencies 1 and 5 Hz) or disrupts (with 10 and 20 Hz) memory performance (Beynel, Appelbaum, et al., 2019). Contrary to the expectations, Brzezicka et al., (2019) in iEEG study demonstrated a negative correlation of theta sourced from DLPFC and WM performance. Thus, a relationship between DLPFC and executive components of WM is still to be established.

The results of stimulations targeting the posterior part of the fronto-parietal network are also inconclusive. The application of 5 Hz rTMS to the left posterior cortex disrupted WM performance but the evidence was weak ($p = 0.045$ in one of the multiple conditions without correction on the number of comparisons) (Beynel, Davis, Crowell, Dannhauer, et al., 2019). Another rTMS study investigated the effects of 1 Hz stimulation of the left supramarginal gyrus on WM (Guidali, Pisoni, Bolognini, & Papagno, 2019). This area of the brain is thought to be related to the maintenance of serial order information. The stimulation hindered performance in the serial recall WM task.

A few studies have tried to establish a causal relationship between successful performance in WM tasks and fronto-parietal network functioning as a whole. Transcranial alternating current stimulation (tACS) technique opens the opportunity to test this hypothesis. tACS oscillating at 6 Hz to the left fronto-parietal improved WM performance (Polanía, Nitsche, Korman, Batsikadze, & Paulus, 2012). Moreover, only in-phase stimulation between the parietal and frontal electrodes had a positive effect, whereas anti-phase stimulation hindered the performance. Although a replication of these effects was not successful (Kleinert, Szymanski, & Müller, 2017), a partial support of these data was provided by two other studies. The first of them demonstrated a positive effect of in-phase stimulation on WM performance as measured by shortened RT (Violante et al., 2017). In the second study desynchronization of parietal and frontal theta led to decreased accuracy and delayed RT (Alekseichuk, Pabel, Antal, & Paulus, 2017). The application of theta tACS to posterior sites with the return electrode placed on the right frontal pole led to an improvement in WM but the montage with the active electrode placed on frontal (F3) site did not (Jaušovec & Jaušovec, 2014; Jaušovec, Jaušovec, & Pahor, 2014). The effect was not replicated in another study by the same group (Pahor & Jaušovec, 2018). Thus, the coordinating role of theta synchronization between the parietal and frontal cortex is partially supported by the non-invasive brain stimulation literature, though contradictory data exist. The area may need more time to establish more convincing evidence.

Numerous studies demonstrated that faster (e.g., gamma) oscillations may occur simultaneously with slower (e.g., theta) oscillations during the performance of WM tasks (Axmacher et al., 2010; Fell & Axmacher, 2011; Kamiński, Brzezicka, & Wróbel, 2011; Roux & Uhlhaas, 2014; Sauseng et al., 2009; Wolinski, Cooper, Sauseng, & Romei, 2018). According to the theta-gamma model of WM, storage of multiple items in WM is executed by nesting gamma cycles within theta oscillations (Lisman & Idiart, 1995; Lisman & Jensen, 2013). One of the theory's predictions is that WM performance is enhanced when gamma cycles are coupled with theta in the upstate phase. Supporting the hypothesis, tACS of synchronized gamma and theta improved WM performance (Alekseichuk, Turi, Amador de Lara, Antal, & Paulus, 2016; Polanía et al., 2012).

The theta-gamma model also postulates that individual items are retained in WM in association with different theta phases. Earlier presented items in a sequence are associated with the earlier phase of theta oscillations. Thus, a longer theta cycle can potentially comprise more gamma cycles and, therefore, more items in WM (see Figure 33). Increasing the number of items in memory led to slowing of theta frequency (Axmacher et al., 2010; Chaieb et al., 2015). The other part of the equation – the frequency of gamma – has been shown to influence individual memory capacity and task performance (Leszczyński et al., 2015). Moreover, theta-to-gamma cycle length ratio in the resting state EEG predicted WM capacity in the task (Kamiński et al., 2011). Slowing down the theta frequency by means of tACS led to improvement in WM performance (Bender, Romei, & Sauseng, 2019; Vosskuhl, Huster, & Herrmann, 2015; Wolinski et al., 2018). In contrast, speeding up the frequency of theta hindered WM (Wolinski et al., 2018).

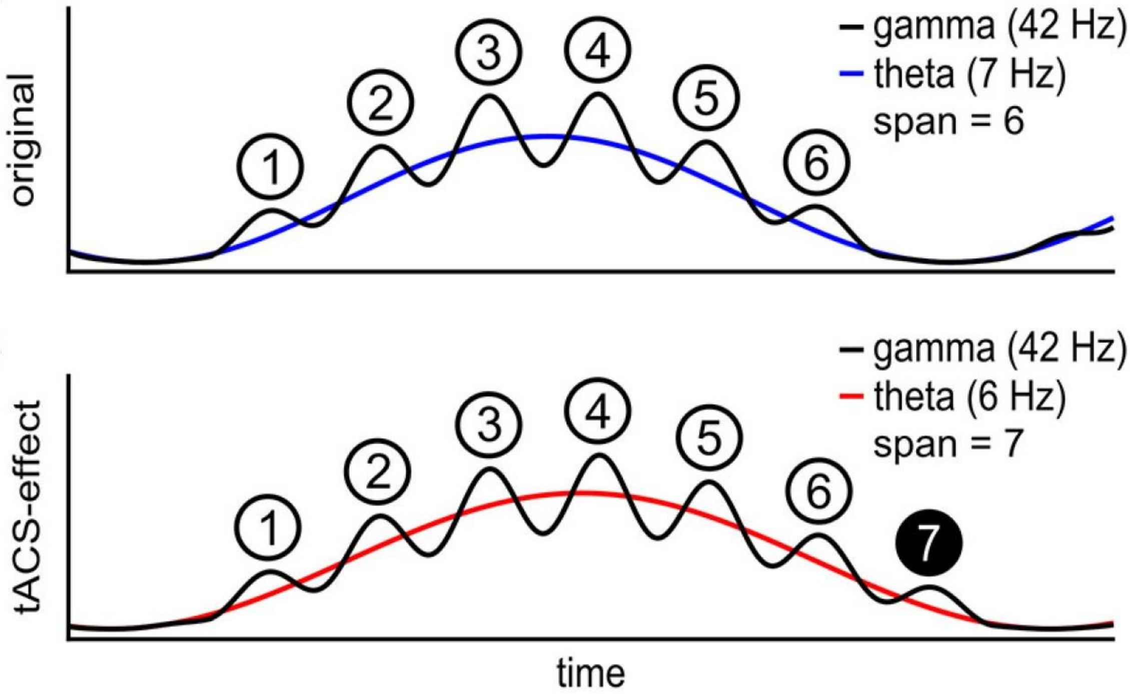

Figure 33 – Theta-gamma coding theory (adopted from Vosskuhl, Huster, & Herrmann, 2015)

The theta-gamma coding model of WM can be partially tested in my data. I correlated the leading theta frequency on individual level and WM performance. Individual theta frequency was defined as the frequency in the 4-8 Hz frequency band with the maximal relative power. The correlation was very close to 0 (rho = 0.004, p = 0.96). Taking into account the power-law (1/f) spectrum of EEG, the methodology used for this calculation may not be optimal. Usage of the absolute theta value is also not perfect for the same reason. A more sophisticated algorithm for the definition of individual theta frequency is needed for more reliable conclusions.

4.4.2 Alpha

The ability to suppress distracting information is a key factor affecting WM performance (Freunberger, Werkle-Bergner, Griesmayr, Lindenberger, & Klimesch, 2011; Gulbinaite, Johnson, de Jong, Morey, & van Rijn, 2014). Sauseng et al. (2009) used the lateralized version of the change detection task. The strength of alpha synchronization in the ipsilateral to the attended hemifield correlated with WM performance, suggesting that the ability to inhibit irrelevant information is important for successful WM performance. Moreover, better behavioral performance (i.e., faster RT) was related to a stronger modulation of alpha in response to distractors presented during WM delay (Bonnefond & Jensen, 2012). The results indicate the role of alpha in the suppression of distracting activity, which is a definitive factor of individual WM capacity. Contradicting Bonneford & Jensen's (2012) conclusions, Roux et al. (2012) obtained a positive relationship between alpha and RT during delay filled with distractors as well as in the most difficult 6-items condition. I tested this hypothesis in my data by correlating alpha with RT in each condition including the same retention of 6 items. No correlation with the performance was found.

Individual differences in accuracy did not affect alpha activity either. The findings of other studies employing similar time-frequency analysis are not very consistent. Thus, Kawasaki & Yamaguchi (2013) reported a negative correlation of visual WM capacity with occipital alpha (N = 14, r = -0.66). In contrast, a positive correlation of verbal WM capacity with posterior alpha demonstrated in another study (N = 13, r = 0.75) (Kwon et al., 2015). Thus, two correlations found in the two studies are both very strong, but with a different sign. A recent verbal WM study explored the correlation of posterior alpha and WM performance (Hu et al., 2019). The authors found that the slope of the modulation of alpha power by WM load ("alpha modulation index") negatively correlated with WM capacity in two samples (N = 20, r = -0.55; N = 23, r = -0.59). In other words, a larger alpha power in more difficult tasks corresponded to better WM performance. A different alpha modulation index was used in two visual studies employing the change detection visual task (Erickson, Smith, Albrecht, & Silverstein, 2019; Fukuda et al., 2015). In these works, the index also negatively correlated with performance (Erickson et al.: N = 60, r = -0.45, Fukuda et al.: N = 28, r = -0.48). A negative alpha modulation index means stronger alpha suppression in the difficult task than in the easy task.

I calculated the alpha modulation index as used in the verbal WM study by Hu et al. (2019) and the test attained significance neither for the overall task performance (r = 0.03, p = 0.72), nor for the retention task only (r = 0.12, p = 0.12). As my data demonstrate, the results obtained in the previous studies are not replicated in a larger sample. One might suggest that the modulation of alpha in high-load conditions as compared with a low-load condition would result in a significant correlation, as opposed to my study where only high-load conditions were employed. If this is true, it would suggest that alpha modulation may be an efficient mechanism to solve WM tasks but only at low to average levels of load.

4.4.3 Beta

Similarly to theta, the beta index of the executive control had a significant relationship with WM performance. The beta suppression was observed during all of the delay period in both tasks. In the manipulation task the magnitude of the suppression was related to WM performance. Not much data is present in the literature concerning relationship between beta activity and individual differences in WM. Probably the only comparable study is a spatial WM MEG experiment published by Proskovec et al. in two articles (Proskovec, Wiesman, Heinrichs-Graham, & Wilson, 2018, 2019). A correlation between beta (15-20 Hz) and behavioral performance was reported in both publications. Although the two papers shared the same sample, WM performance correlated with beta activity localized in completely different areas (the right superior parietal lobule in one paper, and the left DLFPC and the bilateral superior temporal gyrus in the other). The behavioral indexes of WM performance used to calculate the correlations were also substantially different in the two reports. These inconsistencies cast doubt on the reliability of the results. Moreover, the beta effect obtained in the present work had a central distribution, which can hardly be compared with strongly localized beta activities in Proskovec et al.

Similar beta activity characterized the encoding of words to long-term memory in the experiments of Hanslmayr et al. (2011). The strength of beta suppression was associated with a higher probability to remember the word. The beta rhythm had a fronto-central spatial scalp distribution but was related to the BOLD response in the left inferior frontal gyrus (IFG). The IFG has repeatedly been shown to be involved in long-term memory encoding (Kim, 2011). Similarly, the neighboring areas of IFG are involved in encoding to WM (Kim, 2019). Entrainment of the beta activity in IFG by 18.7 Hz rTMS impaired memory in a word-list learning task (Hanslmayr, Matuschek, & Fellner, 2014). The results are suggestive of the role of beta activity in memory formation. The authors hypothesized that beta desynchronization during memory encoding is related to the semantic processing of the words, but this hypothesis contradicts their results that show similar effects of beta entrainment for both semantic and non-semantic conditions. Likewise, no semantic processing was involved in my study. An alternative explanation of the relationship between beta and individual differences in WM is therefore required.

Beta desynchronization may reflect switching internal attention between the reorganized set of letters and the initial set during the manipulations performance. This process may involve prefrontal areas, FEF and the motor cortex. If the beta activity observed in my study is related to activation of motor control networks, then why was it related to individual differences in WM? Repetitive saccade eye movements during delay were shown to increase episodic memory performance (Christman, Garvey, Propper, & Phaneuf, 2003; Lyle & Edlin, 2015). The movements executed just before blocks of an attentional control (Flanker) task also improved performance in the task (Edlin & Lyle, 2013). The attentional enhancement by preactivation of fronto-parietal network nodes such as FEF was hypothesized to produce the above mentioned effects (Edlin & Lyle, 2013). Consistent with this idea, TMS delivered to FEF improved detection of targets in a visuospatial attention task (Grosbras & Paus, 2002), whereas a suppression of the same region by TMS decreased inhibitory control (Muggleton, Chen, Tzeng, Hung, & Juan, 2010). It is admittedly a speculation at this point, but more efficient use of FEF to execute mental manipulations would potentially facilitate WM performance in my study.

4.5 General discussion

In the last section of the discussion, I shall summarize the findings described above in relation to the neural underpinnings of individual differences in WM.

The effect of set-size on neural activity was generally negligent. P3b in retrieval was the only measure that demonstrated a clear load-dependent linear effect. But the P3b effect occurs rather late, when most processing is already done. Neither SCP nor spectral power measures during delay depended substantially on WM load. Despite no changes in the EEG patterns, the accuracy consistently decreased with increasing WM load, but even under the highest load of 7 items remained well above the chance level. Interestingly, there was no indication that participants with different WM capacity operated differently while dealing with increasing set-sizes. Most likely the neural measures employed in my study reached an asymptote below the level of 5 items. This "saturation" phenomenon has been demonstrated in the change detection paradigm by means of contralateral alpha suppression and CDA. A similar effect of the dramatic drop of electrophysiological changes at higher levels of WM load was shown for ERPs in classical versions of the Sternberg task (review of Kotchoubey, 2002). Although the paradigm employed in this study substantially differed from the change detection paradigm, was not a classical Sternberg paradigm and included, besides ERPs, other measures of brain activity, it cannot be ruled out that the same limitation remains valid for my data as well.

A plausible explanation states that above the set-size of 4, the whole set cannot be simultaneously kept in the focus of attention; rather, successful WM is maintained by an additional mechanism of fast switching between the subsets (e.g., the subsets of 3 and 4 items, when the set contains 7 items). Above I already discussed the idea that non-invasive electrophysiological methods may show only the effects directly related to the current focus of attention (which always contains less than five items regardless of the set-size) but not the STM storage per se. A broader range of WM load levels would probably result in better differentiated effects on neural activity.

Introducing the task with manipulations allowed me to survey more closely the neural correlates of working memory in its genuine definition. The effect of task was the most pronounced effect in all studied neural measures. The distinction between Manipulation and Retention conditions had diverse temporal trajectories. It maintained over encoding and delay in SCP, during encoding and the first part of delay in theta, during the first part of delay in beta, and during the whole delay period in alpha. Thus, the power of beta was related to the mental manipulations when visual input is blocked. As indicated by the increased theta power, the executive control of attention starts from the encoding period. Alpha, in turn, is likely to reflect non-specific activation related to the availability of sensory storage and to cognitive stress. The SCP may be affected by a combination of energy demands of the manipulation task on the one hand, and the response preparation processes on the other hand. The temporally distinct mechanisms did not systematically affect the correlation with WM performance. Perhaps, low WM performance may be attributed to a limited access to the executive control or, independently, to restricted visual imagery abilities.

Only spectral power data reliably correlated with individual differences in WM, but ERPs and SCP did not. These results confirm the importance of brain oscillations in the coordination of executive control. As was hypothesized, the executive control ability is the decisive factor influencing WM capacity. I suggest that executive control abilities are essential when the set-size exceeds the average limit of sensory storage of 4 items. The executive control system permits the subjects to rapidly switch attention between different memory representations while keeping the manipulations ongoing. This hypothesis can be tested in a further study including set-sizes both below and above this limit (e.g., 1, 3, 5, and 7 items).

There are several possible mechanisms to explain how executive components of WM may cope with increasing demands on WM, finally determining the individual WM capacity. Camos & Barrouillet (2014) suggested that attention is involved in rapid refreshment of memory traces, thus preventing temporal decay of the WM content. In extension of this model, I assume that the ability to maintain information in the active state by switching the focus of attention between items defines individual capacity limit. The non-refreshed information fades out and in the worst case cannot be recovered. However, there are strong arguments that forgetting is not related to temporal decay (Oberauer et al., 2016). For example, WM capacity measured in the change detection task after a delay interval is the same as measured immediately after encoding, when no decay could have time to occur (Tsubomi, Fukuda, Watanabe, & Vogel, 2013). Severe deterioration of accuracy observed even in short delays makes temporal decay to be unlikely the main factor determining forgetting, and, therefore, the individual capacity limit.

Another function of the central executive, which may be more appropriate for explanation of the individual capacity limit, is protection from interference (Baddeley, 2012). The interference hypothesis assumes that WM performance is affected not only by external distractors but also by mutual interference between the items (Berman et al., 2009; Oberauer et al., 2016, 2018). Thus, the detrimental effect on memory precision is a function of the number of items stored in WM and the presence of the concurrent task. Mind-wandering is an additional source of interference that can affect the precision of WM traces (Teasdale, Proctor, Lloyd, & Baddeley, 1993). Filtering efficiency was hypothesized to be a definitive factor affecting individual WM capacity

(Jost, Bryck, Vogel, & Mayr, 2011; Schwarzkopp, Mayr, & Jost, 2016; Vogel, McCollough, & Machizawa, 2005). Filtering efficiency is the ability to store only task-relevant information in the change detection task. Particularly, older adults with generally worse WM were found to be more susceptible to interference in the task and showed lower 'filtering efficiency' than young adults (Jost et al., 2011).

Alpha rhythm has been proposed as a mechanism participating in protection from interference. Thus Sauseng et al. (2009) demonstrated the importance of increasing alpha activity in the blockade of interfering information. The authors also highlighted the importance of alpha filtering mechanisms in individual differences. However, these findings were not replicated in the current sample. A possible explanation can be the different level of task complexity in this study and in Sauseng et al. (2009). From this viewpoint, alpha filtering mechanism works only under moderate levels of memory load. In more complex conditions, it is the executive control as reflected in theta activity that minimizes the interference, thus determining an individual's WM capacity.

4.6 Conclusions

Studies of individual differences in psychophysiology of WM are uncommon. Several measures have been applied in my dissertation to understand how individual WM capacity is related to underlying neural activity. First of all, large samples are required to tackle the problem of individual differences. A typical number of subjects in WM studies employing EEG is about 20-30 or even less. In the current study the final sample consisted of 156 individuals with close to 50/50 gender balance.

A typical approach in WM research is to use tasks of moderate complexity. This may result in a biased estimation of the difference between high- and low-performers. As the second measure, I increased the variance by application of the above average complexity tasks. This approach has helped to better distinguish between high and low capacity individuals. However, the same factor of above-average complexity might have resulted in the lack of the expected effects of WM load on the retrieval P3b, SCP, and theta and alpha power, which were observed in previous studies.

Third, for the first time a genuine WM task (rather than an STM task) was administered in an EEG study of individual differences. This innovation allowed me to figure out the underlying structure of the nature of the differences between individuals with diverse capacity limits. Although SCP had the expected left fronto-central distribution indicating a link with rehearsal processes, it did not correlate with individual differences in WM. Also P3b was not related to WM performance.

As regards the hypotheses of the study, formulated in the first Chapter, the first of them postulated a close relationship between medial frontal theta and the central executive component of WM. This hypothesis was successfully confirmed, as the data indicate that manipulations in WM strongly enhanced theta activity. In contrast, the hypothesis concerning the role of alpha in the filtering out distractors was not confirmed. Moreover, I could not find evidence for the hypothesis about the role of alpha in WM performance. Instead, lower beta activity in the frequency range of 16-22 Hz emerged as a potential candidate to affect the individual WM capacity; the mechanism of this effect remains unknown. Supposedly, beta oscillations can influence WM performance through regulation of the ability to execute mental manipulations. Finally, the hypothesis postulating that executive components of WM rather than sensory storage plays a decisive role in individual WM capacity limits was confirmed.

Past Failures and Future Directions

In the current work I have presented the most essential and successful part of the work that has been conducted over the past 7 years. The initially collected sample of about 100 subjects resulted in two main findings: (1) there was a correlation between the absolute alpha power and WM performance and (2) females have better WM and larger alpha power. The sample was not gender balanced (67% females), therefore, and I excluded all the males. I wrote a paper using only the females' EEG data (Pavlov & Kotchoubey, 2017. *EEG correlates of working memory performance in females.*), and decided to collect more data to confirm the sex differences in WM and EEG. It had been a long journey to find enough males at the department of psychology in Russia with 1 to 20 female:male ratio. When the desired gender balance was reached, I found that sex differences were no longer statistically significant.

Meanwhile, I was pursuing another idea – to enhance WM performance by means of neurofeedback training. As the first study (in females) demonstrated, the higher frequency alpha power (individual alpha frequency + 2.5 Hz) was an obvious candidate parameter for the training. I conducted such a study. A group of volunteers participated in 6 to 10 sessions of the neurofeedback training. After about 6 months of the data collection on a strict schedule, believe me or not, the results showed no improvement in WM. Even more disappointingly, alpha did not change as well.

This line of work continued in a new direction when I acquired access to a new tool. It was a wonder of the technical progress called a transcranial electrical stimulator, which had arrived in my lab in Russia in 2015. Notably, the method of transcranial electrical stimulation has been known in Russia under different aliases such as electrosleep or transcranial micropolarization for more than a century. Amazingly, it has been in use for many decades in hospitals all around the country without any proper research conducted to prove its efficacy. No FDA or similar agencies' approval is needed in Russia. Actually, with the currents normally used in hospitals (up to 25 mA!) the stimulation might affect cognition. Of course, modern devices do not allow a researcher to do that. I was satisfied with a commonly used 1 mA.

Most importantly, I could apply the alternating currents to stimulate oscillatory brain activity. At the time I already thought that alpha is not the best candidate and that theta is the key to cognitive enhancement. In two experiments, which I finished just a few months ago, I tried to enhance frontal midline theta in the attempt to improve WM. Both experiments showed fascinatingly convincing null effects. Neither manipulation task nor retention task were affected by the stimulation. I plan to publish these data and, probably, give the theta tACS another chance. In some of the previous studies theta tACS improved WM. I am thinking about a systematic comparison of the montage used in my study with the successful ones employed in the previous research.

As an extension of the dissertation, currently I am trying to identify the breaking point of cognitive overload by means of concurrent EEG and pupillometry. This study will help to understand the plateau effect in electrophysiological measures. I am going to track the effect of increasing WM load on brain oscillations on the individual level. I want to know whether the individual trajectories of the change of posterior alpha and frontal midline theta with load may predict behavioral performance. Training on a large sample machine learning classifier will help to solve this task.

The role of theta rhythm in cognition is particularly interesting for me. What I have learned while working on the systematic review is that a few simple modifications in the Sternberg paradigm may help to answer many long-lasting questions. One of the unanswered questions is whether theta rhythm is critical for the maintenance of temporal order. Variation of WM load in wide range starting with the single item load with successive presentation of the stimuli will help to understand the role of theta in maintenance of temporal order. If theta is important to maintain the temporal order, then one item load should lead to the lack of theta activity. A modification of the Sternberg paradigm with the probe requiring maintenance of either the order and content, or only content would help to elucidate how theta is related to the maintenance of temporal order. It would also be interesting to actively vary the duration of the delay period in a wide range. It has been done in behavioral experiments but no electrophysiological studies have systematically studied this question.

References

Aben, B., Stapert, S., & Blokland, A. (2012). About the Distinction between Working Memory and Short-Term Memory. *Frontiers in Psychology*, *3*. https://doi.org/10.3389/fpsyg.2012.00301

Aftanas, L. I., & Golocheikine, S. A. (2001). Human anterior and frontal midline theta and lower alpha reflect emotionally positive state and internalized attention: High-resolution EEG investigation of meditation. *Neuroscience Letters*, *310*(1), 57–60.

Albers, A. M., Kok, P., Toni, I., Dijkerman, H. C., & de Lange, F. P. (2013). Shared Representations for Working Memory and Mental Imagery in Early Visual Cortex. *Current Biology*, *23*(15), 1427–1431. https://doi.org/10.1016/j.cub.2013.05.065

Alekseichuk, I., Pabel, S. C., Antal, A., & Paulus, W. (2017). Intrahemispheric theta rhythm desynchronization impairs working memory. *Restorative Neurology and Neuroscience*, *35*(2), 147–158. https://doi.org/10.3233/RNN-160714

Alekseichuk, I., Turi, Z., Amador de Lara, G., Antal, A., & Paulus, W. (2016). Spatial Working Memory in Humans Depends on Theta and High Gamma Synchronization in the Prefrontal Cortex. *Current Biology*, *26*(12), 1513–1521. https://doi.org/10.1016/j.cub.2016.04.035

Al-Qazzaz, N. K., Bin Mohd Ali, S. H., Ahmad, S. A., Islam, M. S., & Escudero, J. (2015). Selection of Mother Wavelet Functions for Multi-Channel EEG Signal Analysis during a Working Memory Task. *Sensors (Basel)*, *15*(11), 29015–29035. https://doi.org/10.3390/s151129015

Atkinson, R. C., & Shiffrin, R. M. (1968). Human memory: A proposed system and its control processes. In *Psychology of learning and motivation* (Vol. 2, pp. 89–195). Elsevier.

Axmacher, N., Henseler, M. M., Jensen, O., Weinreich, I., Elger, C. E., & Fell, J. (2010). Cross-frequency coupling supports multi-item working memory in the human hippocampus. *Proceedings of the National Academy of Sciences*, *107*(7), 3228–3233. https://doi.org/10.1073/pnas.0911531107

Baayen, R. H. (2004). Statistics in psycholinguistics: A critique of some current gold standards. *Mental Lexicon Working Papers*, *1*(1), 1–47.

Babiloni, C., Babiloni, F., Carducci, F., Cappa, S. F., Cincotti, F., Del Percio, C., … Rossini, P. M. (2004). Human cortical responses during one-bit short-term memory. A high-resolution EEG study on delayed choice reaction time tasks. *Clinical Neurophysiology*, *115*(1), 161–170. https://doi.org/10.1016/S1388-2457(03)00286-4

Backer, K. C., Binns, M. A., & Alain, C. (2015). Neural dynamics underlying attentional orienting to auditory representations in short-term memory. *Journal of Neuroscience*, *35*(3), 1307–1318. https://doi.org/10.1523/jneurosci.1487-14.2015

Baddeley, A. (1996). The fractionation of working memory. *Proceedings of the National Academy of Sciences*, *93*(24), 13468–13472. https://doi.org/10.1073/pnas.93.24.13468

Baddeley, A. (2003). Working memory: Looking back and looking forward. *Nature Reviews Neuroscience*, *4*(10), 829–839. https://doi.org/10.1038/nrn1201

Baddeley, A. (2012). Working Memory: Theories, Models, and Controversies. *Annual Review of Psychology*, *63*(1), 1–29. https://doi.org/10.1146/annurev-psych-120710-100422

Baddeley, A. D., & Hitch, G. (1974). Working memory. In *Psychology of learning and motivation* (Vol. 8, pp. 47–89). Elsevier.

Baddeley, A. D., & Hitch, G. J. (2019). The phonological loop as a buffer store: An update. *Cortex*, *112*, 91–106. https://doi.org/10.1016/j.cortex.2018.05.015

Baddeley, A. D., Hitch, G. J., & Allen, R. J. (2019). From short-term store to multicomponent working memory: The role of the modal model. *Memory & Cognition*, *47*(4), 575–588. https://doi.org/10.3758/s13421-018-0878-5

Bae, G. Y., & Luck, S. J. (2018). Dissociable Decoding of Spatial Attention and Working Memory from EEG Oscillations and Sustained Potentials. *Journal of Neuroscience*, *38*(2), 409–422. https://doi.org/10.1523/jneurosci.2860-17.2017

Bahramisharif, A., Jensen, O., Jacobs, J., & Lisman, J. (2018). Serial representation of items during working memory maintenance at letter-selective cortical sites. *PLOS Biology*, *16*(8), e2003805. https://doi.org/10.1371/journal.pbio.2003805

Bailey, K., Mlynarczyk, G., & West, R. (2016). Slow Wave Activity Related to Working Memory Maintenance in the N-Back Task. *Journal of Psychophysiology*, *30*(4), 141–154. https://doi.org/10.1027/0269-8803/a000164

Barak, O., Tsodyks, M., & Romo, R. (2010). Neuronal Population Coding of Parametric Working Memory. *Journal of Neuroscience*, *30*(28), 9424–9430. https://doi.org/10.1523/JNEUROSCI.1875-10.2010

Barbey, A. K., Koenigs, M., & Grafman, J. (2013). Dorsolateral Prefrontal Contributions to Human Working Memory. *Cortex*, *49*(5), 1195–1205. https://doi.org/10.1016/j.cortex.2012.05.022

Bareš, M., & Rektor, I. (2001). Basal ganglia involvement in sensory and cognitive processing. A depth electrode CNV study in human subjects. *Clinical Neurophysiology*, *112*(11), 2022–2030. https://doi.org/10.1016/S1388-2457(01)00671-X

Barr, D. J. (2013). Random effects structure for testing interactions in linear mixed-effects models. *Frontiers in Psychology*, *4*. https://doi.org/10.3389/fpsyg.2013.00328

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, *68*(3), 255–278.

Barrouillet, P., Bernardin, S., Portrat, S., Vergauwe, E., & Camos, V. (2007). Time and cognitive load in working memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *33*(3), 570–585. https://doi.org/10.1037/0278-7393.33.3.570

Bashivan, P., Bidelman, G. M., & Yeasin, M. (2014). Spectrotemporal dynamics of the EEG during working memory encoding and maintenance predicts individual behavioral capacity. *European Journal of Neuroscience*, *40*(12), 3774–3784. https://doi.org/10.1111/ejn.12749

Basile, L. F. H., Ballester, G., de Castro, C. C., & Gattaz, W. F. (2002). Multifocal slow potential generation revealed by high-resolution EEG and current density reconstruction. *International Journal of Psychophysiology*, *45*(3), 227–240. https://doi.org/10.1016/S0167-8760(02)00014-4

Bastiaansen, M. C. M., Posthuma, D., Groot, P. F. C., & de Geus, E. J. C. (2002). Event-related alpha and theta responses in a visuo-spatial working memory task. *Clinical Neurophysiology*, *113*(12), 1882–1893. https://doi.org/10/ch8zn6

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. *R Package Version*, *1*(7), 1–23.

Bender, M., Romei, V., & Sauseng, P. (2019). Slow Theta tACS of the Right Parietal Cortex Enhances Contralateral Visual Working Memory Capacity. *Brain Topography*, *32*(3), 477–481. https://doi.org/10.1007/s10548-019-00702-2

Benedek, M., Schickel, R. J., Jauk, E., Fink, A., & Neubauer, A. C. (2014). Alpha power increases in right parietal cortex reflects focused internal attention. *Neuropsychologia*, *56*, 393–400. https://doi.org/10.1016/j.neuropsychologia.2014.02.010

Benjamin, D. J., Berger, J. O., Johannesson, M., Nosek, B. A., Wagenmakers, E.-J., Berk, R., … Johnson, V. E. (2018). Redefine statistical significance. *Nature Human Behaviour*, *2*(1), 6–10. https://doi.org/10.1038/s41562-017-0189-z

Berger, B., Griesmayr, B., Minarik, T., Biel, A. L., Pinal, D., Sterr, A., & Sauseng, P. (2019). Dynamic regulation of interregional cortical communication by slow brain oscillations during working memory. *Nature Communications*, *10*(1), 1–11. https://doi.org/10.1038/s41467-019-12057-0

Berger, B., Minarik, T., Griesmayr, B., Stelzig-Schoeler, R., Aichhorn, W., & Sauseng, P. (2016). Brain Oscillatory Correlates of Altered Executive Functioning in Positive and Negative Symptomatic Schizophrenia Patients and Healthy Controls. *Frontiers in Psychology*, *7*. https://doi.org/10.3389/fpsyg.2016.00705

Berger, B., Omer, S., Minarik, T., Sterr, A., & Sauseng, P. (2014). Interacting Memory Systems—Does EEG Alpha Activity Respond to Semantic Long-Term Memory Access in a Working Memory Task? *Biology*, *4*(1), 1–16. https://doi.org/10.3390/biology4010001

Berger, H. (1929). Über das elektrenkephalogramm des menschen. *European Archives of Psychiatry and Clinical Neuroscience*, *87*(1), 527–570.

Berman, M. G., Jonides, J., & Lewis, R. L. (2009). In Search of Decay in Verbal Short-Term Memory. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *35*(2), 317–333. https://doi.org/10.1037/a0014873

Beynel, L., Appelbaum, L. G., Luber, B., Crowell, C. A., Hilbig, S. A., Lim, W., … Deng, Z.-D. (2019). Effects of online repetitive transcranial magnetic stimulation (rTMS) on cognitive processing: A meta-analysis and recommendations for future studies. *Neuroscience & Biobehavioral Reviews*, *107*, 47–58. https://doi.org/10.1016/j.neubiorev.2019.08.018

Beynel, L., Davis, S. W., Crowell, C. A., Dannhauer, M., Lim, W., Palmer, H., … Appelbaum, L. G. (2019). Site-specific effects of online rTMS during a working memory task in healthy older adults. *BioRxiv*. https://doi.org/10.1101/642983

Beynel, L., Davis, S. W., Crowell, C. A., Hilbig, S. A., Lim, W., Nguyen, D., … Appelbaum, L. G. (2018). A systematic study of repetitive transcranial magnetic stimulation to enhance working memory manipulation abilities. *BioRxiv*. https://doi.org/10.1101/278655

Beynel, L., Davis, S. W., Crowell, C. A., Hilbig, S. A., Lim, W., Nguyen, D., … Appelbaum, L. G. (2019). Online repetitive transcranial magnetic stimulation during working memory in younger and older adults: A randomized within-subject comparison. *PLOS ONE*, *14*(3), e0213707. https://doi.org/10.1371/journal.pone.0213707

Birbaumer, N., Elbert, T., Canavan, A. G., & Rockstroh, B. (1990). Slow potentials of the cerebral cortex and behavior. *Physiological Reviews*, *70*(1), 1–41.

Blacker, K. J., Ikkai, A., Lakshmanan, B. M., Ewen, J. B., & Courtney, S. M. (2016). The role of alpha oscillations in deriving and maintaining spatial relations in working memory. *Cognitive, Affective & Behavioral Neuroscience*, *16*(5), 888–901. https://doi.org/10.3758/s13415-016-0439-y

Bonnefond, M., & Jensen, O. (2012). Alpha Oscillations Serve to Protect Working Memory Maintenance against Anticipated Distracters. *Current Biology*, *22*(20), 1969–1974. https://doi.org/10/f4f3h2

Boonstra, T. W., Powell, T. Y., Mehrkanoon, S., & Breakspear, M. (2013). Effects of mnemonic load on cortical activity during visual working memory: Linking ongoing brain activity with evoked responses. *International Journal of Psychophysiology*, *89*(3), 409–418. https://doi.org/10.1016/j.ijpsycho.2013.04.001

Boran, E., Fedele, T., Klaver, P., Hilfiker, P., Stieglitz, L., Grunwald, T., & Sarnthein, J. (2019). Persistent hippocampal neural firing and hippocampal-cortical coupling predict verbal working memory load. *Science Advances*, *5*(3), eaav3687. https://doi.org/10.1126/sciadv.aav3687

Brookes, M. J., Wood, J. R., Stevenson, C. M., Zumer, J. M., White, T. P., Liddle, P. F., & Morris, P. G. (2011). Changes in brain network activity during working memory tasks: A magnetoencephalography study. *NeuroImage*, *55*(4), 1804–1815. https://doi.org/10/fd9gzv

Brown, J. (1958). Some Tests of the Decay Theory of Immediate Memory. *Quarterly Journal of Experimental Psychology*, *10*(1), 12–21. https://doi.org/10.1080/17470215808416249

Brzezicka, A., Kamiński, J., Reed, C. M., Chung, J. M., Mamelak, A. N., & Rutishauser, U. (2019). Working Memory Load-related Theta Power Decreases in Dorsolateral Prefrontal Cortex Predict Individual Differences in Performance. *Journal of Cognitive Neuroscience*, 1–18. https://doi.org/10/gfz6p7

Busch, N. A., & Herrmann, C. S. (2003). Object-load and feature-load modulate EEG in a short-term memory task: *NeuroReport*, *14*(13), 1721–1724. https://doi.org/10.1097/00001756-200309150-00013

Bushman, B. J., & Wells, G. L. (2001). Narrative Impressions of Literature: The Availability Bias and the Corrective Properties of Meta-Analytic Approaches. *Personality and Social Psychology Bulletin*, *27*(9), 1123–1130. https://doi.org/10.1177/0146167201279005

Buzsaki, G. (2004). Neuronal Oscillations in Cortical Networks. *Science*, *304*(5679), 1926–1929. https://doi.org/10.1126/science.1099745

Camos, V., & Barrouillet, P. (2014). Attentional and non-attentional systems in the maintenance of verbal information in working memory: The executive and phonological loops. *Frontiers in Human Neuroscience*, *8*. https://doi.org/10.3389/fnhum.2014.00900

Chaieb, L., Leszczynski, M., Axmacher, N., Höhne, M., Elger, C. E., & Fell, J. (2015). Theta-gamma phase-phase coupling during working memory maintenance in the human hippocampus. *Cognitive Neuroscience*, *6*(4), 149–157. https://doi.org/10.1080/17588928.2015.1058254

Chen, Y., & Huang, X. (2015). Modulation of Alpha and Beta Oscillations during an n-back Task with Varying Temporal Memory Load. *Frontiers in Psychology*, *6*, 2031. https://doi.org/10.3389/fpsyg.2015.02031

Cheng, J., Edwards, L. J., Maldonado-Molina, M. M., Komro, K. A., & Muller, K. E. (2010). Real longitudinal data analysis for real people: Building a good enough mixed model. *Statistics in Medicine*, *29*(4), 504–520. https://doi.org/10.1002/sim.3775

Chou, W. C., Duann, J. R., She, H. C., Huang, L. Y., & Jung, T. P. (2015). Explore the Functional Connectivity between Brain Regions during a Chemistry Working Memory Task. *Plos One*, *10*(6), e0129019. https://doi.org/10.1371/journal.pone.0129019

Christman, S. D., Garvey, K. J., Propper, R. E., & Phaneuf, K. A. (2003). Bilateral eye movements enhance the retrieval of episodic memories. *Neuropsychology*, *17*(2), 221–229. https://doi.org/10.1037/0894-4105.17.2.221

Christophel, T. B., Klink, P. C., Spitzer, B., Roelfsema, P. R., & Haynes, J.-D. (2017). The Distributed Nature of Working Memory. *Trends in Cognitive Sciences*, *21*(2), 111–124. https://doi.org/10.1016/j.tics.2016.12.007

Cohen, J. (1992). A power primer. *Psychological Bulletin*, *112*(1), 155.

Constantinidis, C., Funahashi, S., Lee, D., Murray, J. D., Qi, X.-L., Wang, M., & Arnsten, A. F. T. (2018). Persistent Spiking Activity Underlies Working Memory. *The Journal of Neuroscience*, *38*(32), 7020–7028. https://doi.org/10.1523/JNEUROSCI.2486-17.2018

Conway, A. R., Cowan, N., Bunting, M. F., Therriault, D. J., & Minkoff, S. R. (2002). A latent variable analysis of working memory capacity, short-term memory capacity, processing speed, and general fluid intelligence. *Intelligence*, *30*(2), 163–183.

Conway, A. R., Kane, M. J., Bunting, M. F., Hambrick, D. Z., Wilhelm, O., & Engle, R. W. (2005). Working memory span tasks: A methodological review and user's guide. *Psychonomic Bulletin & Review*, *12*(5), 769–786.

Cowan, N. (1999). An Embedded-Processes Model of Working Memory. In A. Miyake & P. Shah (Eds.), *Models of Working Memory* (pp. 62–101). https://doi.org/10.1017/CBO9781139174909.006

Cowan, N. (2001). The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences*, *24*(1), 87–114. https://doi.org/10.1017/S0140525X01003922

Cowan, N. (2019). Short-term memory based on activated long-term memory: A review in response to Norris (2017). *Psychological Bulletin*, *145*(8), 822–847. https://doi.org/10.1037/bul0000199

Crespo-Garcia, M., Pinal, D., Cantero, J. L., Diaz, F., Zurron, M., & Atienza, M. (2013). Working memory processes are mediated by local and long-range synchronization of alpha oscillations. *Journal of Cognitive Neuroscience*, *25*(8), 1343–1357. https://doi.org/10.1162/jocn_a_00379

Crowley, K. E., & Colrain, I. M. (2004). A review of the evidence for P2 being an independent component process: Age, sleep and modality. *Clinical Neurophysiology*, *115*(4), 732–744. https://doi.org/10.1016/j.clinph.2003.11.021

Curtis, C. E., & D'Esposito, M. (2003). Persistent activity in the prefrontal cortex during working memory. *Trends in Cognitive Sciences*, *7*(9), 415–423. https://doi.org/10.1016/S1364-6613(03)00197-9

Daffner, K. R., Chong, H., Sun, X., Tarbi, E. C., Riis, J. L., McGinnis, S. M., & Holcomb, P. J. (2011). Mechanisms Underlying Age- and Performance-related Differences in Working Memory. *Journal of Cognitive Neuroscience*, *23*(6), 1298–1314. https://doi.org/10.1162/jocn.2010.21540

Dai, Z., de Souza, J., Lim, J., Ho, P. M., Chen, Y., Li, J., … Sun, Y. (2017). EEG Cortical Connectivity Analysis of Working Memory Reveals Topological Reorganization in Theta and Alpha Bands. *Frontiers in Human Neuroscience*, *11*, 237. https://doi.org/10.3389/fnhum.2017.00237

Daneman, M., & Carpenter, P. A. (1980). Individual differences in working memory and reading. *Journal of Verbal Learning and Verbal Behavior*, *19*(4), 450–466. https://doi.org/10.1016/S0022-5371(80)90312-6

Daniel, T. A., Katz, J. S., & Robinson, J. L. (2016). Delayed match-to-sample in working memory: A BrainMap meta-analysis. *Biological Psychology*, *120*, 10–20. https://doi.org/10.1016/j.biopsycho.2016.07.015

de Vries, I. E. J., Driel, J. van, & Olivers, C. N. L. (2017). Posterior α EEG Dynamics Dissociate Current from Future Goals in Working Memory-Guided Visual

Search. *Journal of Neuroscience*, *37*(6), 1591–1603. https://doi.org/10.1523/jneurosci.2945-16.2016

de Vries, I. E. J., van Driel, J., Karacaoglu, M., & Olivers, C. N. L. (2018). Priority Switches in Visual Working Memory are Supported by Frontal Delta and Posterior Alpha Interactions. *Cerebral Cortex*, *28*(11), 4090–4104. https://doi.org/10.1093/cercor/bhy223

Deiber, M.-P., Missonnier, P., Bertrand, O., Gold, G., Fazio-Costa, L., Ibanez, V., & Giannakopoulos, P. (2007). Distinction between perceptual and attentional processing in working memory tasks: A study of phase-locked and induced oscillatory brain dynamics. *Journal of Cognitive Neuroscience*, *19*(1), 158–172.

Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*(1), 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009

D'Esposito, M., Aguirre, G. K., Zarahn, E., Ballard, D., Shin, R. K., & Lease, J. (1998). Functional MRI studies of spatial and nonspatial working memory. *Cognitive Brain Research*, *7*(1), 1–13. https://doi.org/10.1016/S0926-6410(98)00004-4

D'Esposito, M., & Postle, B. R. (2015). The Cognitive Neuroscience of Working Memory. *Annual Review of Psychology*, *66*(1), 115–142. https://doi.org/10.1146/annurev-psych-010814-015031

D'Esposito, M., Postle, B. R., Ballard, D., & Lease, J. (1999). Maintenance versus Manipulation of Information Held in Working Memory: An Event-Related fMRI Study. *Brain and Cognition*, *41*(1), 66–86. https://doi.org/10.1006/brcg.1999.1096

D'Esposito, M., Postle, B. R., & Rypma, B. (2000). Prefrontal cortical contributions to working memory: Evidence from event-related fMRI studies. *Experimental Brain Research*, *133*(1), 3–11. https://doi.org/10.1007/s002210000395

Diekelmann, S., & Born, J. (2010). The memory function of sleep. *Nature Reviews Neuroscience*, *11*(2), 114–126.

Donchin, E., & Coles, M. G. (1988). Is the P300 component a manifestation of context updating? *Behavioral and Brain Sciences*, *11*(3), 357–374. https://doi.org/10.1017/S0140525X00058027

Dong, S., Reder, L. M., Yao, Y., Liu, Y., & Chen, F. (2015). Individual differences in working memory capacity are reflected in different ERP and EEG patterns to task difficulty. *Brain Research*, *1616*, 146–156. https://doi.org/10.1016/j.brainres.2015.05.003

Drew, T., Horowitz, T. S., Wolfe, J. M., & Vogel, E. K. (2011). Delineating the neural signatures of tracking spatial position and working memory during attentive tracking. *Journal of Neuroscience*, *31*(2), 659–668. https://doi.org/10.1523/jneurosci.1339-10.2011

Durup, G., & Fessard, A. (1935). L'électrencéphalogramme de l'homme. Observations psycho-physiologiques relatives à l'action des stimuli visuels et auditifs. *L'année Psychologique*, *36*(1), 1–32.

Eager, C., & Roy, J. (2017). Mixed effects models are sometimes terrible. *ArXiv Preprint ArXiv:1701.04858*.

Edlin, J. M., & Lyle, K. B. (2013). The effect of repetitive saccade execution on the attention network test: Enhancing executive function with a flick of the eyes. *Brain and Cognition*, *81*(3), 345–351. https://doi.org/10.1016/j.bandc.2012.12.006

Ellmore, T. M., Ng, K., & Reichert, C. P. (2017). Early and late components of EEG delay activity correlate differently with scene working memory performance. *Plos One*, *12*(10), e0186072. https://doi.org/10.1371/journal.pone.0186072

Embury, C. M., Wiesman, A. I., Proskovec, A. L., Heinrichs-Graham, E., McDermott, T. J., Lord, G. H., … Wilson, T. W. (2018). Altered Brain Dynamics in Patients With Type 1 Diabetes During Working Memory Processing. *Diabetes*, *67*(6), 1140–1148. https://doi.org/10.2337/db17-1382

Embury, C. M., Wiesman, A. I., Proskovec, A. L., Mills, M. S., Heinrichs-Graham, E., Wang, Y.-P., … Wilson, T. W. (2019). Neural dynamics of verbal working memory processing in children and adolescents. *NeuroImage*, *185*, 191–197. https://doi.org/10.1016/j.neuroimage.2018.10.038

Engel, A. K., & Fries, P. (2010). Beta-band oscillations—Signalling the status quo? *Current Opinion in Neurobiology*, *20*(2), 156–165. https://doi.org/10.1016/j.conb.2010.02.015

Engemann, D. A., Raimondo, F., King, J.-R., Rohaut, B., Louppe, G., Faugeras, F., … Sitt, J. D. (2018). Robust EEG-based cross-site and cross-protocol classification of states of consciousness. *Brain*, *141*(11), 3179–3192. https://doi.org/10.1093/brain/awy251

Engle, R. W. (2002). Working memory capacity as executive attention. *Current Directions in Psychological Science*, *11*(1), 19–23.

Erickson, M. A., Smith, D., Albrecht, M. A., & Silverstein, S. (2019). Alpha-band desynchronization reflects memory-specific processes during visual change detection. *Psychophysiology*, *56*(11). https://doi.org/10.1111/psyp.13442

Eschmann, K. C. J., Bader, R., & Mecklinger, A. (2018). Topographical differences of frontal-midline theta activity reflect functional differences in cognitive control abilities. *Brain and Cognition*, *123*, 57–64. https://doi.org/10.1016/j.bandc.2018.02.002

Fabiani, M., Karis, D., & Donchin, E. (1986). P300 and Recall in an Incidental Memory Paradigm. *Psychophysiology*, *23*(3), 298–308. https://doi.org/10.1111/j.1469-8986.1986.tb00636.x

Fell, J., & Axmacher, N. (2011). The role of phase synchronization in memory processes. *Nature Reviews Neuroscience*, *12*(2), 105–118. https://doi.org/10.1038/nrn2979

Fingelkurts, A. A., Fingelkurts, A. A., Krause, C. M., & Sams, M. (2002). Probability interrelations between pre-/post-stimulus intervals and ERD/ERS during a memory task. *Clinical Neurophysiology*, *113*(6), 826–843. https://doi.org/10.1016/s1388-2457(02)00058-5

Ford, J. M., Roth, W. T., Mohs, R. C., Hopkins, W. F., & Kopell, B. S. (1979). Event-related potentials recorded from young and old adults during a memory retrieval task. *Electroencephalography and Clinical Neurophysiology*, *47*(4), 450–459. https://doi.org/10.1016/0013-4694(79)90161-5

Foster, J. J., Sutterer, D. W., Serences, J. T., Vogel, E. K., & Awh, E. (2016). The topography of alpha-band activity tracks the content of spatial working memory. *Journal of Neurophysiology*, *115*(1), 168–177. https://doi.org/10/gcw8rp

Freunberger, R., Werkle-Bergner, M., Griesmayr, B., Lindenberger, U., & Klimesch, W. (2011). Brain oscillatory correlates of working memory constraints. *Brain Research*, *1375*, 93–102. https://doi.org/10.1016/j.brainres.2010.12.048

Fritz, C. O., Morris, P. E., & Richler, J. J. (2012). Effect size estimates: Current use, calculations, and interpretation. *Journal of Experimental Psychology: General*, *141*(1), 2–18. https://doi.org/10.1037/a0024338

Fukuda, K., Mance, I., & Vogel, E. K. (2015). Alpha Power Modulation and Event-Related Slow Wave Provide Dissociable Correlates of Visual Working Memory. *The Journal of Neuroscience*, *35*(41), 14009–14016. https://doi.org/10.1523/jneurosci.5003-14.2015

Fukuda, K., & Vogel, E. K. (2011). Individual Differences in Recovery Time From Attentional Capture. *Psychological Science*, *22*(3), 361–368. https://doi.org/10.1177/0956797611398493

Funder, D. C., & Ozer, D. J. (2019). Evaluating Effect Size in Psychological Research: Sense and Nonsense. *Advances in Methods and Practices in Psychological Science*, *2*(2), 156–168. https://doi.org/10.1177/2515245919847202

Fuster, J. M., & Alexander, G. E. (1971). Neuron activity related to short-term memory. *Science*, *173*(3997), 652–654. https://doi.org/10.1126/science.173.3997.652

Gao, C., Sun, J., Yang, X., & Gong, H. (2018). Gender differences in brain networks during verbal Sternberg tasks: A simultaneous near-infrared spectroscopy and electro-encephalography study. *Journal of Biophotonics*, *11*(3). https://doi.org/10.1002/jbio.201700120

Gehrig, J., Michalareas, G., Forster, M.-T., Lei, J., Hok, P., Laufs, H., … Kell, C. A. (2019). Low-Frequency Oscillations Code Speech during Verbal Working Memory. *The Journal of Neuroscience*, *39*(33), 6498–6512. https://doi.org/10.1523/JNEUROSCI.0018-19.2019

Getzmann, S., Wascher, E., & Schneider, D. (2018). The role of inhibition for working memory processes: ERP evidence from a short-term storage task. *Psychophysiology*, *55*(5), e13026. https://doi.org/10.1111/psyp.13026

Gevins, A., Smith, M. E., Le, J., Leong, H., Bennett, J., Martin, N., … Whitfield, S. (1996). High resolution evoked potential imaging of the cortical dynamics of human working memory. *Electroencephalography and Clinical Neurophysiology*, *98*(4), 327–348. https://doi.org/10.1016/0013-4694(96)00288-X

Gevins, A., Smith, M. E., McEvoy, L., & Yu, D. (1997). High-resolution EEG mapping of cortical activation related to working memory: Effects of task difficulty, type of processing, and practice. *Cerebral Cortex*, *7*(4), 374–385.

Gignac, G. E. (2014). Fluid intelligence shares closer to 60% of its variance with working memory capacity and is a better indicator of general intelligence. *Intelligence*, *47*, 122–133. https://doi.org/10.1016/j.intell.2014.09.004

Gitelman, D. R., Penny, W. D., Ashburner, J., & Friston, K. J. (2003). Modeling regional and psychophysiologic interactions in fMRI: The importance of hemodynamic deconvolution. *NeuroImage*, *19*(1), 200–207. https://doi.org/10.1016/S1053-8119(03)00058-2

Glahn, D. C., Kim, J., Cohen, M. S., Poutanen, V.-P., Therman, S., Bava, S., … Lönnqvist, J. (2002). Maintenance and Manipulation in Spatial Working Memory: Dissociations in the Prefrontal Cortex. *NeuroImage*, *17*(1), 201–213. https://doi.org/10.1006/nimg.2002.1161

Goldman-Rakic, P. S. (1995). Cellular basis of working memory. *Neuron*, *14*(3), 477–485. https://doi.org/10.1016/0896-6273(95)90304-6

Golob, E. J., & Starr, A. (2004). Visual encoding differentially affects auditory event-related potentials during working memory retrieval. *Psychophysiology*, *41*(2), 186–192. https://doi.org/10.1111/j.1469-8986.2004.00154.x

Gomarus, H. K., Althaus, M., Wijers, A. A., & Minderaa, R. B. (2006). The effects of memory load and stimulus relevance on the EEG during a visual selective memory search task: An ERP and ERD/ERS study. *Clinical Neurophysiology*, *117*(4), 871–884. https://doi.org/10.1016/j.clinph.2005.12.008

Gómez, C. M., Marco, J., & Grau, C. (2003). Preparatory visuo-motor cortical network of the contingent negative variation estimated by current density. *NeuroImage*, *20*(1), 216–224. https://doi.org/10.1016/S1053-8119(03)00295-7

Griesmayr, B., Berger, B., Stelzig-Schoeler, R., Aichhorn, W., Bergmann, J., & Sauseng, P. (2014). EEG theta phase coupling during executive control of visual working memory investigated in individuals with schizophrenia and in healthy controls. *Cognitive, Affective, & Behavioral Neuroscience*, *14*(4), 1340–1355. https://doi.org/10.3758/s13415-014-0272-0

Griesmayr, B., Gruber, W. R., Klimesch, W., & Sauseng, P. (2010). Human frontal midline theta and its synchronization to gamma during a verbal delayed match to sample task. *Neurobiology of Learning and Memory*, *93*(2), 208–215. https://doi.org/10.1016/j.nlm.2009.09.013

Grosbras, M.-H., & Paus, T. (2002). Transcranial Magnetic Stimulation of the Human Frontal Eye Field: Effects on Visual Perception and Attention. *Journal of Cognitive Neuroscience*, *14*(7), 1109–1120. https://doi.org/10.1162/089892902320474553

Grune, K., Metz, A.-M., Hagendorf, H., & Fischer, S. (1996). Information processing in working memory and event-related brain potentials. *International Journal of Psychophysiology*, *23*(1), 111–120. https://doi.org/10.1016/0167-8760(96)00040-2

Guidali, G., Pisoni, A., Bolognini, N., & Papagno, C. (2019). Keeping order in the brain: The supramarginal gyrus and serial order in short-term memory. *Cortex*, *119*, 89–99. https://doi.org/10.1016/j.cortex.2019.04.009

Gulbinaite, R., Johnson, A., de Jong, R., Morey, C. C., & van Rijn, H. (2014). Dissociable mechanisms underlying individual differences in visual working memory capacity. *Neuroimage*, *99*, 197–206. https://doi.org/10.1016/j.neuroimage.2014.05.060

Gulbinaite, R., van Rijn, H., & Cohen, M. X. (2014). Fronto-parietal network oscillations reveal relationship between working memory capacity and cognitive control. *Frontiers in Human Neuroscience*, *8*, 761. https://doi.org/10.3389/fnhum.2014.00761

Hanslmayr, S., Aslan, A., Staudigl, T., Klimesch, W., Herrmann, C. S., & Bäuml, K.-H. (2007). Prestimulus oscillations predict visual perception performance between and within subjects. *NeuroImage*, *37*(4), 1465–1473. https://doi.org/10.1016/j.neuroimage.2007.07.011

Hanslmayr, S., Matuschek, J., & Fellner, M.-C. (2014). Entrainment of Prefrontal Beta Oscillations Induces an Endogenous Echo and Impairs Memory Formation. *Current Biology*, *24*(8), 904–909. https://doi.org/10.1016/j.cub.2014.03.007

Hanslmayr, S., Spitzer, B., & Bäuml, K.-H. (2009). Brain Oscillations Dissociate between Semantic and Nonsemantic Encoding of Episodic Memories. *Cerebral Cortex*, *19*(7), 1631–1640. https://doi.org/10.1093/cercor/bhn197

Harmony, T., Fernandez, T., Silva, J., Bernal, J., Diaz-Comas, L., Reyes, A., … Rodriguez, M. (1996). EEG delta activity: An indicator of attention to internal processing during performance of mental tasks. *International Journal of Psychophysiology*, *24*(1–2), 161–171. https://doi.org/10.1016/S0167-8760(96)00053-0

He, B. J. (2014). Scale-free brain activity: Past, present, and future. *Trends in Cognitive Sciences*, *18*(9), 480–487. https://doi.org/10.1016/j.tics.2014.04.003

Heinrichs-Graham, E., & Wilson, T. W. (2015). Spatiotemporal oscillatory dynamics during the encoding and maintenance phases of a visual working memory task. *Cortex*, *69*, 121–130. https://doi.org/10/f7m9h7

Heinz, A. J., & Johnson, J. S. (2017). Load-Dependent Increases in Delay-Period Alpha-Band Power Track the Gating of Task-Irrelevant Inputs to Working Memory. *Frontiers in Human Neuroscience*, *11*, 250. https://doi.org/10.3389/fnhum.2017.00250

Herding, J., Spitzer, B., & Blankenburg, F. (2016). Upper Beta Band Oscillations in Human Premotor Cortex Encode Subjective Choices in a Vibrotactile Comparison Task. *Journal of Cognitive Neuroscience*, *28*(5), 668–679. https://doi.org/10.1162/jocn_a_00932

Herrmann, C. S., Fründ, I., & Lenz, D. (2010). Human gamma-band activity: A review on cognitive and behavioral correlates and network models. *Neuroscience & Biobehavioral Reviews*, *34*(7), 981–992. https://doi.org/10.1016/j.neubiorev.2009.09.001

Herrmann, C. S., Senkowski, D., & Rottger, S. (2004). Phase-locking and amplitude modulations of EEG alpha: Two measures reflect different cognitive processes in a working memory task. *Experimental Psychology*, *51*(4), 311–318. https://doi.org/10.1027/1618-3169.51.4.311

Hinterberger, T., Veit, R., Strehl, U., Trevorrow, T., Erb, M., Kotchoubey, B., … Birbaumer, N. (2003). Brain areas activated in fMRI during self-regulation of slow cortical potentials (SCPs). *Experimental Brain Research*, *152*(1), 113–122. https://doi.org/10.1007/s00221-003-1515-4

Honkanen, R., Rouhinen, S., Wang, S. H., Palva, J. M., & Palva, S. (2015). Gamma Oscillations Underlie the Maintenance of Feature-Specific Information and the Contents of Visual Working Memory. *Cerebral Cortex*, *25*(10), 3788–3801. https://doi.org/10.1093/cercor/bhu263

Houlihan, M., Stelmack, R., & Campbell, K. (1998). Intelligence and the effects of perceptual processing demands, task difficulty and processing speed on P300, reaction time and movement time. *Intelligence*, *26*(1), 9–25. https://doi.org/10.1016/S0160-2896(99)80049-X

Howard, M. W., Rizzuto, D. S., Caplan, J. B., Madsen, J. R., Lisman, J., Aschenbrenner-Scheibe, R., … Kahana, M. J. (2003). Gamma Oscillations Correlate with Working Memory Load in Humans. *Cerebral Cortex*, *13*(12), 1369–1374. https://doi.org/10/dbw5tp

Hsieh, L. T., Ekstrom, A. D., & Ranganath, C. (2011). Neural oscillations associated with item and temporal order maintenance in working memory. *The Journal of Neuroscience*, *31*(30), 10803–10810. https://doi.org/10.1523/jneurosci.0828-11.2011

Hsieh, L.-T., & Ranganath, C. (2014). Frontal midline theta oscillations during working memory maintenance and episodic encoding and retrieval. *NeuroImage*, *85, Part 2*, 721–729. https://doi.org/10.1016/j.neuroimage.2013.08.003

Hu, Z., Barkley, C. M., Marino, S. E., Wang, C., Rajan, A., Bo, K., … Ding, M. (2019). Working Memory Capacity Is Negatively Associated with Memory Load Modulation of Alpha Oscillations in Retention of Verbal Working Memory. *Journal of Cognitive Neuroscience*, 1–13. https://doi.org/10.1162/jocn_a_01461

Huang, L. Y., She, H. C., Chou, W. C., Chuang, M. H., Duann, J. R., & Jung, T. P. (2013). Brain oscillation and connectivity during a chemistry visual working memory task. *International Journal of Psychophysiology*, *90*(2), 172–179. https://doi.org/10.1016/j.ijpsycho.2013.07.001

Hwang, G., Jacobs, J., Geller, A., Danker, J., Sekuler, R., & Kahana, M. J. (2005). EEG correlates of verbal and nonverbal working memory. *Behavioral and Brain Functions*, *1*, 20. https://doi.org/10.1186/1744-9081-1-20

Ikkai, A., Blacker, K. J., Lakshmanan, B. M., Ewen, J. B., & Courtney, S. M. (2014). Maintenance of relational information in working memory leads to suppression of the sensory cortex. *Journal of Neurophysiology*, *112*(8), 1903–1915. https://doi.org/10.1152/jn.00134.2014

Ioannidis, J. P. A. (2005). Why Most Published Research Findings Are False. *PLOS Medicine*, *2*(8), e124. https://doi.org/10.1371/journal.pmed.0020124

Ishihara, T., & Yoshii, N. (1972). Multivariate analytic study of EEG and mental activity in Juvenile delinquents. *Electroencephalography and Clinical Neurophysiology*, *33*(1), 71–80. https://doi.org/10.1016/0013-4694(72)90026-0

Ishii, R., Shinosaki, K., Ukai, S., Inouye, T., Ishihara, T., Yoshimine, T., … Takeda, M. (1999). Medial prefrontal cortex generates frontal midline theta rhythm. *NeuroReport*, *10*(4), 675. https://doi.org/10.1097/00001756-199903170-00003

Itthipuripat, S., Wessel, J. R., & Aron, A. R. (2013). Frontal theta is a signature of successful working memory manipulation. *Experimental Brain Research*, *224*(2), 255–262. https://doi.org/10.1007/s00221-012-3305-3

Jacobsen, C. F. (1935). Functions of frontal association area in primates. *Archives of Neurology & Psychiatry*, *33*(3), 558–569. https://doi.org/10.1001/archneurpsyc.1935.02250150108009

Jaušovec, N., & Jaušovec, K. (2014). Increasing working memory capacity with theta transcranial alternating current stimulation (tACS). *Biological Psychology*, *96*, 42–47. https://doi.org/10.1016/j.biopsycho.2013.11.006

Jaušovec, N., Jaušovec, K., & Pahor, A. (2014). The influence of theta transcranial alternating current stimulation (tACS) on working memory storage and processing functions. *Acta Psychologica*, *146*, 1–6. https://doi.org/10.1016/j.actpsy.2013.11.011

Jeneson, A., & Squire, L. R. (2011). Working memory, long-term memory, and medial temporal lobe function. *Learning & Memory*, *19*(1), 15–25. https://doi.org/10.1101/lm.024018.111

Jensen, O., Gelfand, J., Kounios, J., & Lisman, J. E. (2002). Oscillations in the alpha band (9-12 Hz) increase with memory load during retention in a short-term memory task. *Cerebral Cortex*, *12*(8), 877–882. https://doi.org/10.1093/cercor/12.8.877

Jensen, O., & Mazaheri, A. (2010). Shaping Functional Architecture by Oscillatory Alpha Activity: Gating by Inhibition. *Frontiers in Human Neuroscience*, *4*. https://doi.org/10.3389/fnhum.2010.00186

Jensen, O., & Tesche, C. D. (2002). Frontal theta activity in humans increases with memory load in a working memory task. *European Journal of Neuroscience*, *15*(8), 1395–1399.

Jerbi, K., Ossandón, T., Hamamé, C. M., Senova, S., Dalal, S. S., Jung, J., … Lachaux, J.-P. (2009). Task-related gamma-band dynamics from an intracerebral perspective: Review and implications for surface EEG and MEG. *Human Brain Mapping*, *30*(6), 1758–1771. https://doi.org/10.1002/hbm.20750

Jerde, T. A., Merriam, E. P., Riggall, A. C., Hedges, J. H., & Curtis, C. E. (2012). Prioritized Maps of Space in Human Frontoparietal Cortex. *Journal of Neuroscience*, *32*(48), 17382–17390. https://doi.org/10.1523/JNEUROSCI.3810-12.2012

Johnson, J. S., Sutterer, D. W., Acheson, D. J., Lewis-Peacock, J. A., & Postle, B. R. (2011). Increased Alpha-Band Power during the Retention of Shapes and Shape-Location Associations in Visual Short-Term Memory. *Frontiers in Psychology*, *2*, 128. https://doi.org/10.3389/fpsyg.2011.00128

Jost, K., Bryck, R. L., Vogel, E. K., & Mayr, U. (2011). Are Old Adults Just Like Low Working Memory Young Adults? Filtering Efficiency and Age Differences in Visual Working Memory. *Cerebral Cortex*, *21*(5), 1147–1154. https://doi.org/10.1093/cercor/bhq185

Jung, K.-Y., Kim, S. M., Song, J.-Y., Lee, B. U., Lee, C., Lee, S. K., … Kim, K. H. (2015). Sternberg working memory performance following treatment with pramipexole in patients with moderate-to-severe restless legs syndrome. *Sleep Medicine*, *16*(6), 703–708. https://doi.org/10.1016/j.sleep.2014.10.025

Kambara, T., Brown, E. C., Jeong, J.-W., Ofen, N., Nakai, Y., & Asano, E. (2017). Spatio-temporal dynamics of working memory maintenance and scanning of verbal information. *Clinical Neurophysiology*, *128*(6), 882–891. https://doi.org/10.1016/j.clinph.2017.03.005

Kamiński, J., Brzezicka, A., & Wróbel, A. (2011). Short-term memory capacity (7±2) predicted by theta to gamma cycle length ratio. *Neurobiology of Learning and Memory*, *95*(1), 19–23. https://doi.org/10.1016/j.nlm.2010.10.001

Kamiński, J., & Rutishauser, U. (2019). Between persistently active and activity-silent frameworks: Novel vistas on the cellular basis of working memory. *Annals of the New York Academy of Sciences*, nyas.14213. https://doi.org/10.1111/nyas.14213

Kane, M. J., Conway, A. R. A., Hambrick, D. Z., & Engle, R. W. (2008). Variation in Working Memory Capacity as Variation in Executive Attention and Control. In A. Conway, C. Jarrold, M. Kane, A. Miyake, & J. Towse (Eds.), *Variation in Working Memory* (pp. 21–48). https://doi.org/10.1093/acprof:oso/9780195168648.003.0002

Kane, M. J., Hambrick, D. Z., & Conway, A. R. A. (2005). Working Memory Capacity and Fluid Intelligence Are Strongly Related Constructs: Comment on Ackerman, Beier, and Boyle (2005). *Psychological Bulletin*, *131*(1), 66–71. https://doi.org/10.1037/0033-2909.131.1.66

Karis, D., Fabiani, M., & Donchin, E. (1984). "P300" and memory: Individual differences in the von Restorff effect. *Cognitive Psychology*, *16*(2), 177–216. https://doi.org/10.1016/0010-0285(84)90007-0

Kawasaki, M., Kitajo, K., & Yamaguchi, Y. (2010). Dynamic links between theta executive functions and alpha storage buffers in auditory and visual working memory. *European Journal of Neuroscience*, *31*(9), 1683–1689. https://doi.org/10.1111/j.1460-9568.2010.07217.x

Kawasaki, M., & Watanabe, M. (2007). Oscillatory gamma and theta activity during repeated mental manipulations of a visual image. *Neuroscience Letters*, *422*(2), 141–145. https://doi.org/10.1016/j.neulet.2007.04.079

Kawasaki, M., & Yamaguchi, Y. (2012). Individual visual working memory capacities and related brain oscillatory activities are modulated by color preferences. *Frontiers in Human Neuroscience*, *6*, 318. https://doi.org/10.3389/fnhum.2012.00318

Kawasaki, M., & Yamaguchi, Y. (2013). Frontal theta and beta synchronizations for monetary reward increase visual working memory capacity. *Social Cognitive and Affective Neuroscience*, *8*(5), 523–530. https://doi.org/10.1093/scan/nss027

Khader, P. H., Jost, K., Ranganath, C., & Rosler, F. (2010). Theta and alpha oscillations during working-memory maintenance predict successful long-term memory encoding. *Neuroscience Letters*, *468*(3), 339–343. https://doi.org/10.1016/j.neulet.2009.11.028

Khader, P., Ranganath, C., Seemüller, A., & Rösler, F. (2007). Working memory maintenance contributes to long-term memory formation: Evidence from slow event-related brain potentials. *Cognitive, Affective, & Behavioral Neuroscience*, *7*(3), 212–224. https://doi.org/10.3758/CABN.7.3.212

Khader, P., Schicke, T., Röder, B., & Rösler, F. (2008). On the relationship between slow cortical potentials and BOLD signal changes in humans. *International*

Journal of Psychophysiology, *67*(3), 252–261. https://doi.org/10.1016/j.ijpsycho.2007.05.018

Kim, H. (2011). Neural activity that predicts subsequent memory and forgetting: A meta-analysis of 74 fMRI studies. *NeuroImage*, *54*(3), 2446–2461. https://doi.org/10.1016/j.neuroimage.2010.09.045

Kim, H. (2019). Neural activity during working memory encoding, maintenance, and retrieval: A network-based model and meta-analysis. *Human Brain Mapping*, *40*(17), 4912–4933. https://doi.org/10.1002/hbm.24747

Kim, S. M., Choi, J. W., Lee, C., Lee, B. U., Koo, Y. S., Kim, K. H., & Jung, K.-Y. (2014). Working memory deficit in patients with restless legs syndrome: An event-related potential study. *Sleep Medicine*, *15*(7), 808–815. https://doi.org/10.1016/j.sleep.2014.03.010

Kleinert, M.-L., Szymanski, C., & Müller, V. (2017). Frequency-Unspecific Effects of θ-tACS Related to a Visuospatial Working Memory Task. *Frontiers in Human Neuroscience*, *11*. https://doi.org/10.3389/fnhum.2017.00367

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: A review and analysis. *Brain Research Reviews*, *29*(2), 169–195.

Klimesch, W., Doppelmayr, M., Schwaiger, J., Auinger, P., & Winkler, T. (1999). “Paradoxical” alpha synchronization in a memory task. *Brain Research. Cognitive Brain Research*, *7*(4), 493–501. https://doi.org/10.1016/S0926-6410(98)00056-1

Klimesch, W., Freunberger, R., & Sauseng, P. (2010). Oscillatory mechanisms of process binding in memory. *Neuroscience and Biobehavioral Reviews*, *34*(7), 1002–1014. https://doi.org/10.1016/j.neubiorev.2009.10.004

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition–timing hypothesis. *Brain Research Reviews*, *53*(1), 63–88. https://doi.org/10.1016/j.brainresrev.2006.06.003

Klimesch, W., Schimke, H., & Pfurtscheller, G. (1993). Alpha frequency, cognitive load and memory performance. *Brain Topography*, *5*(3), 241–251. https://doi.org/10.1007/BF01128991

Kloosterman, N. A., Meindertsma, T., Hillebrand, A., van Dijk, B. W., Lamme, V. A. F., & Donner, T. H. (2014). Top-down modulation in human visual cortex predicts the stability of a perceptual illusion. *Journal of Neurophysiology*, *113*(4), 1063–1076. https://doi.org/10.1152/jn.00338.2014

Kofler, M. J., Rapport, M. D., Bolden, J., Sarver, D. E., & Raiker, J. S. (2010). ADHD and Working Memory: The Impact of Central Executive Deficits and Exceeding Storage/Rehearsal Capacity on Observed Inattentive Behavior. *Journal of Abnormal Child Psychology*, *38*(2), 149–161. https://doi.org/10.1007/s10802-009-9357-6

Kok, A. (2001). On the utility of P3 amplitude as a measure of processing capacity. *Psychophysiology*, *38*(3), 557–577.

Konecky, R. O., Smith, M. A., & Olson, C. R. (2017). Monkey prefrontal neurons during Sternberg task performance: Full contents of working memory or most recent item? *Journal of Neurophysiology*, *117*(6), 2269–2281. https://doi.org/10.1152/jn.00541.2016

Kotchoubey, B. (2002). Do Event-Related Brain Potentials Reflect Mental (Cognitive) Operations? *Journal of Psychophysiology*, *16*(3), 129–149. https://doi.org/10.1027//0269-8803.16.3.129

Kotchoubey, B. I., Jordan, J. S., Grozinger, B., Westphal, K. P., & Kornhuber, H. H. (1996). Event-related brain potentials in a varied-set memory search task: A reconsideration. *Psychophysiology*, *33*(5), 530–540. https://doi.org/10.1111/j.1469-8986.1996.tb02429.x

Kottlow, M., Schlaepfer, A., Baenninger, A., Michels, L., Brandeis, D., & Koenig, T. (2015). Pre-stimulus BOLD-network activation modulates EEG spectral activity during working memory retention. *Frontiers in Behavioral Neuroscience*, *9*, 111. https://doi.org/10.3389/fnbeh.2015.00111

Kumar, S., Joseph, S., Gander, P. E., Barascud, N., Halpern, A. R., & Griffiths, T. D. (2016). A brain system for auditory working memory. *Journal of Neuroscience*, *36*(16), 4492–4505. https://doi.org/10.1523/JNEUROSCI.4341-14.2016

Kustermann, T., Popov, T., Miller, G. A., & Rockstroh, B. (2018). Verbal working memory-related neural network communication in schizophrenia. *Psychophysiology*, *55*(9). https://doi.org/10.1111/psyp.13088

Kustermann, T., Rockstroh, B., Miller, G. A., & Popov, T. (2018). Neural network communication facilitates verbal working memory. *Biological Psychology*, *136*, 119–126. https://doi.org/10.1016/j.biopsycho.2018.05.018

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, *82*(13). https://doi.org/10.18637/jss.v082.i13

Kwon, G., Lim, S., Kim, M. Y., Kwon, H., Lee, Y. H., Kim, K., … Suh, M. (2015). Individual differences in oscillatory brain activity in response to varying attentional demands during a word recall and oculomotor dual task. *Frontiers in Human Neuroscience*, *9*, 381. https://doi.org/10.3389/fnhum.2015.00381

Lachaux, J.-P., Axmacher, N., Mormann, F., Halgren, E., & Crone, N. E. (2012). High-frequency neural activity and human cognition: Past, present and possible future of intracranial EEG research. *Progress in Neurobiology*, *98*(3), 279–301. https://doi.org/10.1016/j.pneurobio.2012.06.008

Larocque, J. J., Lewis-Peacock, J. A., & Postle, B. R. (2014). Multiple neural states of representation in short-term memory? It’s a matter of attention. *Frontiers in Human Neuroscience*, *8*, 5. https://doi.org/10.3389/fnhum.2014.00005

Lefebvre, C. D., Marchand, Y., Eskes, G. A., & Connolly, J. F. (2005). Assessment of working memory abilities using an event-related brain potential (ERP)-compatible digit span backward task. *Clinical Neurophysiology*, *116*(7), 1665–1680. https://doi.org/10.1016/j.clinph.2005.03.015

Leiberg, S., Lutzenberger, W., & Kaiser, J. (2006). Effects of memory load on cortical oscillatory activity during auditory pattern working memory. *Brain Research*, *1120*(1), 131–140. https://doi.org/10/cw492t

Leijten, F. S. S., Huiskamp, G.-J. M., Hilgersom, I., & van Huffelen, A. C. (2003). High-resolution Source Imaging in Mesiotemporal Lobe Epilepsy: A Comparison Between MEG and Simultaneous EEG. *Journal of Clinical Neurophysiology*, *20*(4), 227. https://doi.org/10.1097/00004691-200307000-00001

Lenartowicz, A., Delorme, A., Walshaw, P. D., Cho, A. L., Bilder, R. M., McGough, J. J., … Loo, S. K. (2014). Electroencephalography correlates of spatial working memory deficits in attention-deficit/hyperactivity disorder: Vigilance, encoding, and maintenance. *The Journal of Neuroscience*, *34*(4), 1171–1182. https://doi.org/10.1523/JNEUROSCI.1765-13.2014

Leszczyński, M., Fell, J., & Axmacher, N. (2015). Rhythmic Working Memory Activation in the Human Hippocampus. *Cell Reports*, *13*(6), 1272–1282. https://doi.org/10.1016/j.celrep.2015.09.081

Lewandowsky, S., Oberauer, K., & Brown, G. D. A. (2009). No temporal decay in verbal short-term memory. *Trends in Cognitive Sciences*, *13*(3), 120–126. https://doi.org/10.1016/j.tics.2008.12.003

Lewis-Peacock, J. A., Drysdale, A. T., Oberauer, K., & Postle, B. R. (2011). Neural Evidence for a Distinction between Short-term Memory and the Focus of Attention. *Journal of Cognitive Neuroscience*, *24*(1), 61–79. https://doi.org/10.1162/jocn_a_00140

Linden, D. E. J. (2007). The Working Memory Networks of the Human Brain. *The Neuroscientist*, *13*(3), 257–267. https://doi.org/10.1177/1073858406298480

Lindquist, M. A., Meng Loh, J., Atlas, L. Y., & Wager, T. D. (2009). Modeling the hemodynamic response function in fMRI: Efficiency, bias and mis-modeling. *NeuroImage*, *45*(1, Supplement 1), S187–S198. https://doi.org/10.1016/j.neuroimage.2008.10.065

Lisman, J. E., & Idiart, M. A. (1995). Storage of 7 +/- 2 short-term memories in oscillatory subcycles. *Science*, *267*(5203), 1512–1515. https://doi.org/10.1126/science.7878473

Lisman, J. E., & Jensen, O. (2013). The Theta-Gamma Neural Code. *Neuron*, *77*(6), 1002–1016. https://doi.org/10.1016/j.neuron.2013.03.007

Liu, D., Guo, C., & Luo, J. (2010). An electrophysiological analysis of maintenance and manipulation in working memory. *Neuroscience Letters*, *482*(2), 123–127. https://doi.org/10.1016/j.neulet.2010.07.015

Liu, M., Zhou, L., Wang, X., Jiang, Y., & Liu, Q. (2017). Deficient manipulation of working memory in remitted depressed individuals: Behavioral and electrophysiological evidence. *Clinical Neurophysiology*, *128*(7), 1206–1213. https://doi.org/10.1016/j.clinph.2017.04.011

Liu, S., Poh, J. H., Koh, H. L., Ng, K. K., Loke, Y. M., Lim, J. K. W., … Zhou, J. (2018). Carrying the past to the future: Distinct brain networks underlie individual differences in human spatial working memory capacity. *Neuroimage*, *176*, 1–10. https://doi.org/10.1016/j.neuroimage.2018.04.014

Logothetis, N. K., Pauls, J., Augath, M., Trinath, T., & Oeltermann, A. (2001). Neurophysiological investigation of the basis of the fMRI signal. *Nature*, *412*(6843), 150–157. https://doi.org/10.1038/35084005

Lopez-Calderon, J., & Luck, S. J. (2014). ERPLAB: An open-source toolbox for the analysis of event-related potentials. *Frontiers in Human Neuroscience*, *8*, 213. https://doi.org/10.3389/fnhum.2014.00213

Lorist, M. M., Snel, J., Mulder, G., & Kok, A. (1995). Aging, caffeine, and information processing: An event-related potential analysis. *Electroencephalography and Clinical Neurophysiology*, *96*(5), 453–467. https://doi.org/10.1016/0168-5597(95)00069-5

Luck, S. J. (2014). *An Introduction to the Event-Related Potential Technique*. MIT Press.

Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature*, *390*(6657), 279–281. https://doi.org/10.1038/36846

Luria, R., Balaban, H., Awh, E., & Vogel, E. K. (2016). The contralateral delay activity as a neural measure of visual working memory. *Neuroscience and Biobehavioral Reviews*, *62*, 100–108. https://doi.org/10.1016/j.neubiorev.2016.01.003

Lyle, K. B., & Edlin, J. M. (2015). Why does saccade execution increase episodic memory retrieval? A test of the top-down attentional control hypothesis. *Memory*, *23*(2), 187–202. https://doi.org/10.1080/09658211.2013.877487

Ma, Q., Hu, L., Li, J., Hu, Y., Xia, L., Chen, X., & Hu, W. (2016). Different Effects of Hypoxia on Mental Rotation of Normal and Mirrored Letters: Evidence from the Rotation-Related Negativity. *PLOS ONE*, *11*(5), e0154479. https://doi.org/10.1371/journal.pone.0154479

MacCallum, R. C., Zhang, S., Preacher, K. J., & Rucker, D. D. (2002). On the practice of dichotomization of quantitative variables. *Psychological Methods*, *7*(1), 19–40. https://doi.org/10.1037/1082-989X.7.1.19

Mainy, N., Kahane, P., Minotti, L., Hoffmann, D., Bertrand, O., & Lachaux, J. P. (2007). Neural correlates of consolidation in working memory. *Human Brain Mapping*, *28*(3), 183–193. https://doi.org/10.1002/hbm.20264

Malmivuo, J. (2012). Comparison of the Properties of EEG and MEG in Detecting the Electric Activity of the Brain. *Brain Topography*, *25*(1), 1–19. https://doi.org/10.1007/s10548-011-0202-1

Manohar, S. G., Zokaei, N., Fallon, S. J., Vogels, T. P., & Husain, M. (2019). Neural mechanisms of attending to items in working memory. *Neuroscience &*

Biobehavioral Reviews, *101*, 1–12. https://doi.org/10.1016/j.neubiorev.2019.03.017

Manza, P., Hau, C. L., & Leung, H. C. (2014). Alpha power gates relevant information during working memory updating. *The Journal of Neuroscience*, *34*(17), 5998–6002. https://doi.org/10.1523/jneurosci.4641-13.2014

Mapelli, I., & Ozkurt, T. E. (2019). Brain Oscillatory Correlates of Visual Short-Term Memory Errors. *Frontiers in Human Neuroscience*, *13*, 33. https://doi.org/10.3389/fnhum.2019.00033

Marsh, G. R. (1975). Age differences in evoked potential correlates of a memory scanning process. *Experimental Aging Research*, *1*(1), 3–16. https://doi.org/10.1080/03610737508257942

Maurer, U., Brem, S., Liechti, M., Maurizio, S., Michels, L., & Brandeis, D. (2015). Frontal midline theta reflects individual task performance in a working memory task. *Brain Topography*, *28*(1), 127–134. https://doi.org/10.1007/s10548-014-0361-y

McCallum, W. C., & Curry, S. H. (2013). *Slow Potential Changes in the Human Brain*. Springer Science & Business Media.

McDermott, T. J., Badura-Brack, A. S., Becker, K. M., Ryan, T. J., Khanna, M. M., Heinrichs-Graham, E., & Wilson, T. W. (2016). Male veterans with PTSD exhibit aberrant neural dynamics during working memory processing: An MEG study. *Journal of Psychiatry & Neuroscience : JPN*, *41*(4), 251–260. https://doi.org/10.1503/jpn.150058

McEvoy, L. K., Smith, M. E., & Gevins, A. (1998). Dynamic cortical networks of verbal and spatial working memory: Effects of memory load and task practice. *Cerebral Cortex*, *8*(7), 563–574. https://doi.org/10.1093/cercor/8.7.563

Mecklinger, A., & Pfeifer, E. (1996). Event-related potentials reveal topographical and temporal distinct neuronal activation patterns for spatial and object working memory. *Cognitive Brain Research*, *4*(3), 211–224. https://doi.org/10.1016/S0926-6410(96)00034-1

Melnik, N., Mapelli, I., & Ozkurt, T. E. (2017). Modulation of alpha oscillations is required for the suppression of semantic interference. *Neurobiology of Learning and Memory*, *144*, 11–18. https://doi.org/10.1016/j.nlm.2017.05.007

Meltzer, J. A., Negishi, M., Mayes, L. C., & Constable, R. T. (2007). Individual differences in EEG theta and alpha dynamics during working memory correlate with fMRI responses across subjects. *Clinical Neurophysiology*, *118*(11), 2419–2436.

Meltzer, J. A., Zaveri, H. P., Goncharova, I. I., Distasio, M. M., Papademetris, X., Spencer, S. S., … Constable, R. T. (2008). Effects of Working Memory Load on Oscillatory Power in Human Intracranial EEG. *Cerebral Cortex*, *18*(8), 1843–1855. https://doi.org/10/bfmnb9

Michels, L., Bucher, K., Lüchinger, R., Klaver, P., Martin, E., Jeanmonod, D., & Brandeis, D. (2010). Simultaneous EEG-fMRI during a Working Memory Task: Modulations in Low and High Frequency Bands. *PLoS ONE*, *5*(4), e10298. https://doi.org/10.1371/journal.pone.0010298

Michels, L., Lüchinger, R., Koenig, T., Martin, E., & Brandeis, D. (2012). Developmental Changes of BOLD Signal Correlations with Global Human EEG Power and Synchronization during Working Memory. *PLOS ONE*, *7*(7), e39447. https://doi.org/10/f337r3

Michels, L., Moazami-Goudarzi, M., Jeanmonod, D., & Sarnthein, J. (2008). EEG alpha distinguishes between cuneal and precuneal activation in working memory. *NeuroImage*, *40*(3), 1296–1310. https://doi.org/10.1016/j.neuroimage.2007.12.048

Miller, G. A. (1956). The magical number seven, plus or minus two: Some limits on our capacity for processing information. *Psychological Review*, *63*(2), 81.

Miller, J., & Ulrich, R. (2019). The quest for an optimal alpha. *PLOS ONE*, *14*(1), e0208631. https://doi.org/10.1371/journal.pone.0208631

Mitchell, D. J., McNaughton, N., Flanagan, D., & Kirk, I. J. (2008). Frontal-midline theta from the perspective of hippocampal "theta." *Progress in Neurobiology*, *86*(3), 156–185. https://doi.org/10.1016/j.pneurobio.2008.09.005

Mizuhara, H., Wang, L.-Q., Kobayashi, K., & Yamaguchi, Y. (2004). A long-range cortical network emerging with theta oscillation in a mental task. *NeuroReport*, *15*(8), 1233. https://doi.org/10.1097/01.wnr.0000126755.09715.b3

Moher, D., Liberati, A., Tetzlaff, J., & Altman, D. G. (2009). Preferred reporting items for systematic reviews and meta-analyses: The PRISMA statement. *Annals of Internal Medicine*, *151*(4), 264–269. https://doi.org/10/bpq5

Monfort, V., & Pouthas, V. (2003). Effects of working memory demands on frontal slow waves in time-interval reproduction tasks in humans. *Neuroscience Letters*, *343*(3), 195–199. https://doi.org/10.1016/S0304-3940(03)00385-9

Morrison, C., Kamal, F., & Taler, V. (2019). The influence of working memory performance on event-related potentials in young and older adults. *Cognitive Neuroscience*, *10*(3), 117–128. https://doi.org/10.1080/17588928.2019.1570104

Muggleton, N. G., Chen, C.-Y., Tzeng, O. J. L., Hung, D. L., & Juan, C.-H. (2010). Inhibitory Control and the Frontal Eye Fields. *Journal of Cognitive Neuroscience*, *22*(12), 2804–2812. https://doi.org/10.1162/jocn.2010.21416

Münte, T. F., Schiltz, K., & Kutas, M. (1998). When temporal terms belie conceptual order. *Nature*, *395*(6697), 71–73. https://doi.org/10.1038/25731

Murphy, K., Roodenrys, S., & Fox, A. (2006). Event-related potential correlates of the word length effect in working memory. *Brain Research*, *1112*(1), 179–190. https://doi.org/10.1016/j.brainres.2006.07.007

Muthukumaraswamy, S. (2013). High-frequency brain activity and muscle artifacts in MEG/EEG: A review and recommendations. *Frontiers in Human Neuroscience*, *7*. https://doi.org/10.3389/fnhum.2013.00138

Myers, N. E., Walther, L., Wallis, G., Stokes, M. G., & Nobre, A. C. (2015). Temporal dynamics of attention during encoding versus maintenance of working memory: Complementary views from event-related potentials and alpha-band oscillations. *Journal of Cognitive Neuroscience*, *27*(3), 492–508. https://doi.org/10.1162/jocn_a_00727

Narayanan, N. S., Prabhakaran, V., Bunge, S. A., Christoff, K., Fine, E. M., & Gabrieli, J. D. E. (2005). The Role of the Prefrontal Cortex in the Maintenance of Verbal Working Memory: An Event-Related fMRI Analysis. *Neuropsychology*, *19*(2), 223–232. https://doi.org/10.1037/0894-4105.19.2.223

Nee, D. E., Brown, J. W., Askren, M. K., Berman, M. G., Demiralp, E., Krawitz, A., & Jonides, J. (2013). A Meta-analysis of Executive Components of Working Memory. *Cerebral Cortex*, *23*(2), 264–282. https://doi.org/10.1093/cercor/bhs007

Nee, D. E., & Jonides, J. (2013). Trisecting representational states in short-term memory. *Frontiers in Human Neuroscience*, *7*. https://doi.org/10.3389/fnhum.2013.00796

Nenert, R., Viswanathan, S., Dubuc, D. M., & Visscher, K. M. (2012). Modulations of ongoing alpha oscillations predict successful short-term visual memory encoding. *Frontiers in Human Neuroscience*, *6*, 127. https://doi.org/10.3389/fnhum.2012.00127

Nichols, E. A., Kao, Y.-C., Verfaellie, M., & Gabrieli, J. D. E. (2006). Working memory and long-term memory for faces: Evidence from fMRI and global amnesia for involvement of the medial temporal lobes. *Hippocampus*, *16*(7), 604–616. https://doi.org/10.1002/hipo.20190

Nigbur, R., Ivanova, G., & Stürmer, B. (2011). Theta power as a marker for cognitive interference. *Clinical Neurophysiology*, *122*(11), 2185–2194. https://doi.org/10.1016/j.clinph.2011.03.030

Norris, D. (2017). Short-term memory and long-term memory are still different. *Psychological Bulletin*, *143*(9), 992–1009. https://doi.org/10.1037/bul0000108

Norris, D. (2019). Even an activated long-term memory system still needs a separate short-term store: A reply to Cowan (2019). *Psychological Bulletin*, *145*(8), 848–853. https://doi.org/10.1037/bul0000204

Nulsen, C. E., Fox, A. M., & Hammond, G. R. (2010). Processes contributing to forward and backward span: An ERP investigation: *NeuroReport*, *21*(4), 298–302. https://doi.org/10.1097/WNR.0b013e32833730f0

Nyhus, E., & Curran, T. (2010). Functional Role of Gamma and Theta Oscillations in Episodic Memory. *Neuroscience and Biobehavioral Reviews*, *34*(7), 1023–1035. https://doi.org/10.1016/j.neubiorev.2009.12.014

Oberauer, K. (2002). Access to information in working memory: Exploring the focus of attention. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *28*(3), 411. https://doi.org/10.1037/0278-7393.28.3.411

Oberauer, K., Farrell, S., Jarrold, C., & Lewandowsky, S. (2016). What limits working memory capacity? *Psychological Bulletin*, *142*(7), 758.

Oberauer, K., Lewandowsky, S., Awh, E., Brown, G. D., Conway, A., Cowan, N., … Hurlstone, M. J. (2018). Benchmarks for models of short-term and working memory. *Psychological Bulletin*, *144*(9), 885.

Oberauer, K., Schulze, R., Wilhelm, O., & Süß, H.-M. (2005). Working Memory and Intelligence--Their Correlation and Their Relation: Comment on Ackerman, Beier, and Boyle (2005). *Psychological Bulletin*, *131*(1), 61–65. https://doi.org/10.1037/0033-2909.131.1.61

Oberauer, K., Süß, H.-M., Schulze, R., Wilhelm, O., & Wittmann, W. W. (2000). Working memory capacity—Facets of a cognitive ability construct. *Personality and Individual Differences*, *29*(6), 1017–1045. https://doi.org/10.1016/S0191-8869(99)00251-2

Okuhata, S., Kusanagi, T., & Kobayashi, T. (2013). Parietal EEG alpha suppression time of memory retrieval reflects memory load while the alpha power of memory maintenance is a composite of the visual process according to simultaneous and successive Sternberg memory tasks. *Neuroscience Letters*, *555*, 79–84. https://doi.org/10.1016/j.neulet.2013.09.010

Olson, I. R. (2006). Working Memory for Conjunctions Relies on the Medial Temporal Lobe. *Journal of Neuroscience*, *26*(17), 4596–4601. https://doi.org/10.1523/JNEUROSCI.1923-05.2006

Onton, J., Delorme, A., & Makeig, S. (2005). Frontal midline EEG dynamics during working memory. *NeuroImage*, *27*(2), 341–356. https://doi.org/10.1016/j.neuroimage.2005.04.014

Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, *2011*, 1.

Pae, C.-U. (2015). Why Systematic Review rather than Narrative Review? *Psychiatry Investigation*, *12*(3), 417–419. https://doi.org/10.4306/pi.2015.12.3.417

Pahor, A., & Jausovec, N. (2017). Multifaceted pattern of neural efficiency in working memory capacity. *Intelligence*, *65*, 23–34. https://doi.org/10.1016/j.intell.2017.10.001

Pahor, A., & Jaušovec, N. (2018). The Effects of Theta and Gamma tACS on Working Memory and Electrophysiology. *Frontiers in Human Neuroscience*, *11*. https://doi.org/10.3389/fnhum.2017.00651

Palmer, J. A., Kreutz-Delgado, K., & Makeig, S. (2012). AMICA: An adaptive mixture of independent component analyzers with shared components. *Swartz Center for Computatonal Neursoscience, University of California San Diego, Tech. Rep*. Retrieved from https://sccn.ucsd.edu/~jason/amica_a.pdf

Palomaki, J., Kivikangas, M., Alafuzoff, A., Hakala, T., & Krause, C. M. (2012). Brain oscillatory 4-35 Hz EEG responses during an n-back task with complex visual stimuli. *Neuroscience Letters*, *516*(1), 141–145. https://doi.org/10.1016/j.neulet.2012.03.076

Palva, J. M., Monto, S., Kulashekhar, S., & Palva, S. (2010). Neuronal synchrony reveals working memory networks and predicts individual memory capacity. *Proceedings of the National Academy of Sciences*, *107*(16), 7580–7585. https://doi.org/10.1073/pnas.0913113107

Park, H. D., Min, B. K., & Lee, K. M. (2010). EEG oscillations reflect visual short-term memory processes for the change detection in human faces. *Neuroimage*, *53*(2), 629–637. https://doi.org/10.1016/j.neuroimage.2010.06.057

Park, J. Y., Jhung, K., Lee, J., & An, S. K. (2013). Theta-gamma coupling during a working memory task as compared to a simple vigilance task. *Neuroscience Letters*, *532*, 39–43. https://doi.org/10.1016/j.neulet.2012.10.061

Pasternak, T., & Greenlee, M. W. (2005). Working memory in primate sensory systems. *Nature Reviews Neuroscience*, *6*(2), 97–107. https://doi.org/10.1038/nrn1603

Pavlov, Y. G., & Kotchoubey, B. (2017). EEG correlates of working memory performance in females. *BMC Neuroscience*, *18*(1), 26. https://doi.org/10.1186/s12868-017-0344-5

Pavlov, Y. G., & Kotchoubey, B. (2019). Classical conditioning in oddball paradigm: A comparison between aversive and name conditioning. *Psychophysiology*, e13370. https://doi.org/10.1111/psyp.13370

Payne, L., & Sekuler, R. (2014). The Importance of Ignoring: Alpha Oscillations Protect Selectivity. *Current Directions in Psychological Science*, *23*(3), 171–177. https://doi.org/10/f57hd7

Pelosi, L., Hayward, M., & Blumhardt, L. D. (1995). Is “memory-scanning” time in the Sternberg paradigm reflected in the latency of event-related potentials?

Electroencephalography and Clinical Neurophysiology, *96*(1), 44–55. https://doi.org/10.1016/0013-4694(94)00163-F

Pesonen, M., Hämäläinen, H., & Krause, C. M. (2007). Brain oscillatory 4–30 Hz responses during a visual n-back memory task with varying memory load. *Brain Research*, *1138*, 171–177. https://doi.org/10.1016/j.brainres.2006.12.076

Peterson, L., & Peterson, M. J. (1959). Short-term retention of individual verbal items. *Journal of Experimental Psychology*, *58*(3), 193–198. https://doi.org/10.1037/h0049234

Pfurtscheller, G., Brunner, C., Schlögl, A., & Lopes da Silva, F. H. (2006). Mu rhythm (de)synchronization and EEG single-trial classification of different motor imagery tasks. *NeuroImage*, *31*(1), 153–159. https://doi.org/10.1016/j.neuroimage.2005.12.003

Pfurtscheller, G., & Da Silva, F. L. (1999). Event-related EEG/MEG synchronization and desynchronization: Basic principles. *Clinical Neurophysiology*, *110*(11), 1842–1857.

Pfurtscheller, G., & Neuper, C. (1997). Motor imagery activates primary sensorimotor area in humans. *Neuroscience Letters*, *239*(2–3), 65–68. https://doi.org/10.1016/S0304-3940(97)00889-6

Pfurtscheller, G., Stancak, A., & Neuper, C. (1996). Event-related synchronization (ERS) in the alpha band—an electrophysiological correlate of cortical idling: A review. *International Journal of Psychophysiology*, *24*(1), 39–46.

Pizzagalli, D. A., Oakes, T. R., & Davidson, R. J. (2003). Coupling of theta activity and glucose metabolism in the human rostral anterior cingulate cortex: An EEG/PET study of normal and depressed subjects. *Psychophysiology*, *40*(6), 939–949. https://doi.org/10.1111/1469-8986.00112

Poch, C., Campo, P., Parmentier, F. B. R., Ruiz-Vargas, J. M., Elsley, J. V., Castellanos, N. P., … del Pozo, F. (2010). Explicit processing of verbal and spatial features during letter-location binding modulates oscillatory activity of a fronto-parietal network. *Neuropsychologia*, *48*(13), 3846–3854. https://doi.org/10.1016/j.neuropsychologia.2010.09.015

Poch, C., Valdivia, M., Capilla, A., Hinojosa, J. A., & Campo, P. (2018). Suppression of no-longer relevant information in Working Memory: An alpha-power related mechanism? *Biological Psychology*, *135*, 112–116. https://doi.org/10.1016/j.biopsycho.2018.03.009

Polanía, R., Nitsche, M. A., Korman, C., Batsikadze, G., & Paulus, W. (2012). The Importance of Timing in Segregated Theta Phase-Coupling for Cognitive Performance. *Current Biology*, *22*(14), 1314–1318. https://doi.org/10.1016/j.cub.2012.05.021

Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*, *118*(10), 2128–2148.

Postle, B. R. (2006). Working memory as an emergent property of the mind and brain. *Neuroscience*, *139*(1), 23–38. https://doi.org/10.1016/j.neuroscience.2005.06.005

Postle, B. R., Ferrarelli, F., Hamidi, M., Feredoes, E., Massimini, M., Peterson, M., … Tononi, G. (2006). Repetitive Transcranial Magnetic Stimulation Dissociates Working Memory Manipulation from Retention Functions in the Prefrontal, but not Posterior Parietal, Cortex. *Journal of Cognitive Neuroscience*, *18*(10), 11.

Predovan, D., Prime, D., Arguin, M., Gosselin, F., Dell'acqua, R., & Jolicoeur, P. (2009). On the representation of words and nonwords in visual short-term memory: Evidence from human electrophysiology. *Psychophysiology*, *46*(1), 191–199. https://doi.org/10.1111/j.1469-8986.2008.00753.x

Prime, D., Dell'acqua, R., Arguin, M., Gosselin, F., & Jolicoeur, P. (2011). Spatial layout of letters in nonwords affects visual short-term memory load: Evidence from human electrophysiology. *Psychophysiology*, *48*(3), 430–436. https://doi.org/10.1111/j.1469-8986.2010.01072.x

Prime, D. J., & Jolicoeur, P. (2010). Mental rotation requires visual short-term memory: Evidence from human electric cortical activity. *Journal of Cognitive Neuroscience*, *22*(11), 2437–2446. https://doi.org/10.1162/jocn.2009.21337

Pritchard, W. S. (1992). The Brain in Fractal Time: 1/F-Like Power Spectrum Scaling of the Human Electroencephalogram. *International Journal of Neuroscience*, *66*(1–2), 119–129. https://doi.org/10.3109/00207459208999796

Proskovec, A. L., Heinrichs-Graham, E., & Wilson, T. W. (2016). Aging modulates the oscillatory dynamics underlying successful working memory encoding and maintenance. *Human Brain Mapping*, *37*(6), 2348–2361. https://doi.org/10.1002/hbm.23178

Proskovec, A. L., Heinrichs-Graham, E., & Wilson, T. W. (2019). Load modulates the alpha and beta oscillatory dynamics serving verbal working memory. *NeuroImage*, *184*, 256–265. https://doi.org/10.1016/j.neuroimage.2018.09.022

Proskovec, A. L., Wiesman, A. I., Heinrichs-Graham, E., & Wilson, T. W. (2018). Beta Oscillatory Dynamics in the Prefrontal and Superior Temporal Cortices Predict Spatial Working Memory Performance. *Scientific Reports*, *8*(1), 8488. https://doi.org/10/gdp4ww

Proskovec, A. L., Wiesman, A. I., Heinrichs-Graham, E., & Wilson, T. W. (2019). Load effects on spatial working memory performance are linked to distributed alpha and beta oscillations. *Human Brain Mapping*. https://doi.org/10.1002/hbm.24625

R Core Team. (2013). *R: A language and environment for statistical computing*.

Raghavachari, S., Kahana, M. J., Rizzuto, D. S., Caplan, J. B., Kirschen, M. P., Bourgeois, B., … Lisman, J. E. (2001). Gating of human theta oscillations by a working memory task. *The Journal of Neuroscience*, *21*(9), 3175–3183.

Rahm, B., Kaiser, J., Unterrainer, J. M., Simon, J., & Bledowski, C. (2014). FMRI characterization of visual working memory recognition. *NeuroImage*, *90*, 413–422. https://doi.org/10.1016/j.neuroimage.2013.12.017

Rajsic, J., Burton, J. A., & Woodman, G. F. (2019). Contralateral delay activity tracks the storage of visually presented letters and words. *Psychophysiology*, *56*(1), e13282. https://doi.org/10.1111/psyp.13282

Ranganath, C., Cohen, M. X., & Brozinsky, C. J. (2005). Working Memory Maintenance Contributes to Long-term Memory Formation: Neural and Behavioral Evidence. *Journal of Cognitive Neuroscience*, *17*(7), 994–1010. https://doi.org/10.1162/0898929054475118

Ranganath, C., DeGutis, J., & D'Esposito, M. (2004). Category-specific modulation of inferior temporal activity during working memory encoding and maintenance. *Cognitive Brain Research*, *20*(1), 37–45. https://doi.org/10.1016/j.cogbrainres.2003.11.017

Rawle, C. J., Miall, R. C., & Praamstra, P. (2012). Frontoparietal theta activity supports behavioral decisions in movement-target selection. *Frontiers in Human Neuroscience*, *6*, 138. https://doi.org/10.3389/fnhum.2012.00138

Richardson, J. T. (2011). Eta squared and partial eta squared as measures of effect size in educational research. *Educational Research Review*, *6*(2), 135–147.

Ricker, T. J., & Cowan, N. (2010). Loss of Visual Working Memory within Seconds: The Combined Use of Refreshable and Non-Refreshable Features. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *36*(6), 1355–1368. https://doi.org/10.1037/a0020356

Ricker, T. J., Spiegel, L. R., & Cowan, N. (2014). Time-based loss in visual short-term memory is from trace decay, not temporal distinctiveness. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *40*(6), 1510–1523. https://doi.org/10.1037/xlm0000018

Riggall, A. C., & Postle, B. R. (2012). The Relationship between Working Memory Storage and Elevated Activity as Measured with Functional Magnetic Resonance Imaging. *Journal of Neuroscience*, *32*(38), 12990–12998. https://doi.org/10.1523/JNEUROSCI.1892-12.2012

Roberts, B. M., Hsieh, L. T., & Ranganath, C. (2013). Oscillatory activity during maintenance of spatial and temporal information in working memory. *Neuropsychologia*, *51*(2), 349–357. https://doi.org/10.1016/j.neuropsychologia.2012.10.009

Román-López, T. V., Caballero-Sánchez, U., Cisneros-Luna, S., Franco-Rodríguez, J. A., Méndez-Díaz, M., Prospéro-García, O., & Ruiz-Contreras, A. E. (2019). Brain electrical activity from encoding to retrieval while maintaining and manipulating information in working memory. *Memory*, *0*(0), 1–16. https://doi.org/10.1080/09658211.2019.1620287

Rose, N. S., LaRocque, J. J., Riggall, A. C., Gosseries, O., Starrett, M. J., Meyering, E. E., & Postle, B. R. (2016). Reactivation of latent working memories with transcranial magnetic stimulation. *Science*, *354*(6316), 1136–1139. https://doi.org/10.1126/science.aah7011

Roth, W. T., Kopell, B. S., Tinklenberg, J. R., Darley, C. F., Sikora, R., & Vesecky, T. B. (1975). The contingent negative variation during a memory retrieval task. *Electroencephalography and Clinical Neurophysiology*, *38*(2), 171–174. https://doi.org/10.1016/0013-4694(75)90226-6

Roth, W. T., Rothbart, R. M., & Kopell, B. S. (1978). The timing of CNV resolution in a memory retrieval task. *Biological Psychology*, *6*(1), 39–49. https://doi.org/10.1016/0301-0511(78)90005-4

Roux, F., & Uhlhaas, P. J. (2014). Working memory and neural oscillations: Alpha-gamma versus theta-gamma codes for distinct WM information? *Trends in Cognitive Sciences*, *18*(1), 16–25. https://doi.org/10.1016/j.tics.2013.10.010

Roux, F., Wibral, M., Mohr, H. M., Singer, W., & Uhlhaas, P. J. (2012). Gamma-Band Activity in Human Prefrontal Cortex Codes for the Number of Relevant Items Maintained in Working Memory. *Journal of Neuroscience*, *32*(36), 12411–12420. https://doi.org/10/f38nxd

Ruchkin, D. S., Berndt, R. S., Johnson, R., Grafman, J., Ritter, W., & Canoune, H. L. (1999). Lexical Contributions to Retention of Verbal Information in Working Memory: Event-Related Brain Potential Evidence. *Journal of Memory and Language*, *41*(3), 345–364. https://doi.org/10.1006/jmla.1999.2644

Ruchkin, D. S., Berndt, R. S., Johnson, R., Ritter, W., Grafman, J., & Canoune, H. L. (1997). Modality-specific processing streams in verbal working memory: Evidence from spatio-temporal patterns of brain activity. *Brain Research. Cognitive Brain Research*, *6*(2), 95–113.

Ruchkin, D. S., Canoune, H. L., Johnson, R., & Ritter, W. (1995). Working memory and preparation elicit different patterns of slow wave event-related brain potentials. *Psychophysiology*, *32*(4), 399–410. https://doi.org/10.1111/j.1469-8986.1995.tb01223.x

Ruchkin, D. S., Grafman, J., Cameron, K., & Berndt, R. S. (2003). Working memory retention systems: A state of activated long-term memory. *Behavioral and Brain Sciences*, *26*(6), 709–728. https://doi.org/10.1017/S0140525X03000165

Ruchkin, D. S., Grafman, J., Krauss, G. L., Johnson, R., Canoune, H., & Ritter, W. (1994). Event-related brain potential evidence for a verbal working memory deficit in multiple sclerosis. *Brain*, *117*(2), 289–305. https://doi.org/10.1093/brain/117.2.289

Ruchkin, D. S., Johnson, R., Canoune, H., & Ritter, W. (1990). Short-term memory storage and retention: An event-related brain potential study.

Electroencephalography and Clinical Neurophysiology, *76*(5), 419–439. https://doi.org/10.1016/0013-4694(90)90096-3

Ruchkin, D. S., Johnson, R., Grafman, J., Canoune, H., & Ritter, W. (1992). Distinctions and similarities among working memory processes: An event-related potential study. *Cognitive Brain Research*, *1*(1), 53–66. https://doi.org/10.1016/0926-6410(92)90005-C

Ruchkin, D. S., Johnson, R., Grafman, J., Canoune, H., & Ritter, W. (1997). Multiple visuospatial working memory buffers: Evidence from spatiotemporal patterns of brain activity. *Neuropsychologia*, *35*(2), 195–209. https://doi.org/10.1016/S0028-3932(96)00068-1

Rushby, J. A., Barry, R. J., & Johnstone, S. J. (2002). Event-related potential correlates of serial-position effects during an elaborative memory test. *International Journal of Psychophysiology*, *46*(1), 13–27. https://doi.org/10.1016/s0167-8760(02)00037-5

Sauseng, P., Griesmayr, B., Freunberger, R., & Klimesch, W. (2010). Control mechanisms in working memory: A possible function of EEG theta oscillations. *Neuroscience & Biobehavioral Reviews*, *34*(7), 1015–1022. https://doi.org/10.1016/j.neubiorev.2009.12.006

Sauseng, P., Hoppe, J., Klimesch, W., Gerloff, C., & Hummel, F. C. (2007). Dissociation of sustained attention from central executive functions: Local activity and interregional connectivity in the theta range. *European Journal of Neuroscience*, *25*(2), 587–593. https://doi.org/10.1111/j.1460-9568.2006.05286.x

Sauseng, P., Klimesch, W., Doppelmayr, M., Pecherstorfer, T., Freunberger, R., & Hanslmayr, S. (2005). EEG alpha synchronization and functional coupling during top-down processing in a working memory task. *Human Brain Mapping*, *26*(2), 148–155. https://doi.org/10.1002/hbm.20150

Sauseng, P., Klimesch, W., Heise, K. F., Gruber, W. R., Holz, E., Karim, A. A., … Hummel, F. C. (2009). Brain Oscillatory Substrates of Visual Short-Term Memory Capacity. *Current Biology*, *19*(21), 1846–1852. https://doi.org/10.1016/j.cub.2009.08.062

Sauseng, P., Klimesch, W., Schabus, M., & Doppelmayr, M. (2005). Fronto-parietal EEG coherence in theta and upper alpha reflect central executive functions of working memory. *International Journal of Psychophysiology*, *57*(2), 97–103. https://doi.org/10.1016/j.ijpsycho.2005.03.018

Schack, B., & Klimesch, W. (2002). Frequency characteristics of evoked and oscillatory electroencephalic activity in a human memory scanning task. *Neuroscience Letters*, *331*(2), 107–110. https://doi.org/10/b8b5kc

Scharinger, C., Soutschek, A., Schubert, T., & Gerjets, P. (2017). Comparison of the Working Memory Load in N-Back and Working Memory Span Tasks by Means of EEG Frequency Band Power and P300 Amplitude. *Frontiers in Human Neuroscience*, *11*, 6. https://doi.org/10.3389/fnhum.2017.00006

Scheeringa, R., Bastiaansen, M. C. M., Petersson, K. M., Oostenveld, R., Norris, D. G., & Hagoort, P. (2008). Frontal theta EEG activity correlates negatively with the default mode network in resting state. *International Journal of Psychophysiology*, *67*(3), 242–251. https://doi.org/10.1016/j.ijpsycho.2007.05.017

Scheeringa, R., Petersson, K. M., Oostenveld, R., Norris, D. G., Hagoort, P., & Bastiaansen, M. C. M. (2009). Trial-by-trial coupling between EEG and BOLD identifies networks related to alpha and theta EEG power increases during working memory maintenance. *NeuroImage*, *44*(3), 1224–1238. https://doi.org/10.1016/j.neuroimage.2008.08.041

Schmidt, T. T., & Blankenburg, F. (2018). Brain regions that retain the spatial layout of tactile stimuli during working memory – A 'tactospatial sketchpad'? *NeuroImage*, *178*, 531–539. https://doi.org/10.1016/j.neuroimage.2018.05.076

Schmidt, T. T., Wu, Y., & Blankenburg, F. (2017). Content-Specific Codes of Parametric Vibrotactile Working Memory in Humans. *The Journal of Neuroscience*, *37*(40), 9771–9777. https://doi.org/10.1523/JNEUROSCI.1167-17.2017

Schneider, D., Barth, A., & Wascher, E. (2017). On the contribution of motor planning to the retroactive cuing benefit in working memory: Evidence by mu and beta oscillatory activity in the EEG. *Neuroimage*, *162*, 73–85. https://doi.org/10.1016/j.neuroimage.2017.08.057

Schneider, D., Goddertz, A., Haase, H., Hickey, C., & Wascher, E. (2019). Hemispheric asymmetries in EEG alpha oscillations indicate active inhibition during attentional orienting within working memory. *Behavioural Brain Research*, *359*, 38–46. https://doi.org/10.1016/j.bbr.2018.10.020

Schneider, D., Mertes, C., & Wascher, E. (2015). On the fate of non-cued mental representations in visuo-spatial working memory: Evidence by a retro-cuing paradigm. *Behavioural Brain Research*, *293*, 114–124. https://doi.org/10.1016/j.bbr.2015.07.034

Schwarzkopp, T., Mayr, U., & Jost, K. (2016). Early Selection versus Late Correction: Age-Related Differences in Controlling Working Memory Contents. *Psychology and Aging*, *31*(5), 430–441. https://doi.org/10.1037/pag0000103

Seemuller, A., Muller, E. M., & Rosler, F. (2012). EEG-power and -coherence changes in a unimodal and a crossmodal working memory task with visual and kinesthetic stimuli. *Int J Psychophysiol*, *83*(1), 87–95. https://doi.org/10.1016/j.ijpsycho.2011.10.009

Serences, J. T., Ester, E. F., Vogel, E. K., & Awh, E. (2009). Stimulus-Specific Delay Activity in Human Primary Visual Cortex. *Psychological Science*, *20*(2), 207–214. https://doi.org/10.1111/j.1467-9280.2009.02276.x

Sharon, D., Hämäläinen, M. S., Tootell, R. B. H., Halgren, E., & Belliveau, J. W. (2007). The advantage of combining MEG and EEG: Comparison to fMRI in focally stimulated visual cortex. *NeuroImage*, *36*(4), 1225–1235. https://doi.org/10.1016/j.neuroimage.2007.03.066

Shipstead, Z., Lindsey, D. R. B., Marshall, R. L., & Engle, R. W. (2014). The mechanisms of working memory capacity: Primary memory, secondary memory, and attention control. *Journal of Memory and Language*, *72*, 116–141. https://doi.org/10.1016/j.jml.2014.01.004

Silvanto, J. (2017). Working Memory Maintenance: Sustained Firing or Synaptic Mechanisms? *Trends in Cognitive Sciences*, *21*(3), 152–154. https://doi.org/10.1016/j.tics.2017.01.009

Silva-Pereyra, J., Fernández, T., Harmony, T., Bernal, J., Galán, L., Díaz-Comas, L., … Marosi, E. (2001). Delayed P300 during Sternberg and color discrimination tasks in poor readers. *International Journal of Psychophysiology*, *40*(1), 17–32. https://doi.org/10.1016/S0167-8760(00)00123-9

Simmons, J. P., Nelson, L. D., & Simonsohn, U. (2011). False-positive psychology: Undisclosed flexibility in data collection and analysis allows presenting anything as significant. *Psychological Science*, *22*(11), 1359–1366.

Smith, E. E., & Jonides, J. (1999). Storage and executive processes in the frontal lobes. *Science*, *283*(5408), 1657–1661. https://doi.org/10.1126/science.283.5408.1657

Smyrnis, N., Protopapa, F., Tsoukas, E., Balogh, A., Siettos, C. I., & Evdokimidis, I. (2014). Amplitude spectrum EEG signal evidence for the dissociation of motor and perceptual spatial working memory in the human brain. *Experimental Brain Research*, *232*(2), 659–673. https://doi.org/10.1007/s00221-013-3774-z

Speer, M. E., & Soldan, A. (2015). Cognitive reserve modulates ERPs associated with verbal working memory in healthy younger and older adults. *Neurobiology of Aging*, *36*(3), 1424–1434. https://doi.org/10.1016/j.neurobiolaging.2014.12.025

Sperling, G. (1960). The information available in brief visual presentations. *Psychological Monographs: General and Applied*, *74*(11), 1–29. https://doi.org/10.1037/h0093759

Spitzer, B., & Blankenburg, F. (2012). Supramodal Parametric Working Memory Processing in Humans. *The Journal of Neuroscience*, *32*(10), 3287–3295. https://doi.org/10.1523/JNEUROSCI.5280-11.2012

Spitzer, B., Fleck, S., & Blankenburg, F. (2014). Parametric alpha- and beta-band signatures of supramodal numerosity information in human working memory. *The Journal of Neuroscience*, *34*(12), 4293–4302. https://doi.org/10.1523/jneurosci.4580-13.2014

Spitzer, B., Gloel, M., Schmidt, T. T., & Blankenburg, F. (2014). Working memory coding of analog stimulus properties in the human prefrontal cortex. *Cerebral Cortex*, *24*(8), 2229–2236. https://doi.org/10.1093/cercor/bht084

Spitzer, B., & Haegens, S. (2017). Beyond the status Quo: A role for beta oscillations in endogenous content (Re-) activation. *Eneuro*, ENEURO–0170.

Spitzer, B., Wacker, E., & Blankenburg, F. (2010). Oscillatory correlates of vibrotactile frequency processing in human working memory. *The Journal of Neuroscience*, *30*(12), 4496–4502. https://doi.org/10.1523/jneurosci.6041-09.2010

Sprague, T. C., Ester, E. F., & Serences, J. T. (2014). Reconstructions of Information in Visual Spatial Working Memory Degrade with Memory Load. *Current Biology*, *24*(18), 2174–2180. https://doi.org/10.1016/j.cub.2014.07.066

Stefan, H., Schüler, P., Abraham-Fuchs, K., Schneider, S., Gebhardt, M., Neubauer, U., … Thierauf, P. (1994). Magnetic source localization and morphological changes in temporal lobe epilepsy: Comparison of MEG/EEG, ECoG and volumetric MRI in presurgical evaluation of operated patients. *Acta Neurologica Scandinavica*, *89*(S152), 83–88. https://doi.org/10.1111/j.1600-0404.1994.tb05192.x

Steinbrink, J., Villringer, A., Kempf, F., Haux, D., Boden, S., & Obrig, H. (2006). Illuminating the BOLD signal: Combined fMRI–fNIRS studies. *Magnetic Resonance Imaging*, *24*(4), 495–505. https://doi.org/10.1016/j.mri.2005.12.034

Stephane, M., Ince, N. F., Kuskowski, M., Leuthold, A., Tewfik, A. H., Nelson, K., … Tadipatri, V. A. (2010). Neural oscillations associated with the primacy and recency effects of verbal working memory. *Neuroscience Letters*, *473*(3), 172–177. https://doi.org/10.1016/j.neulet.2010.02.025

Sternberg, S. (1966). High-speed scanning in human memory. *Science*, *153*(3736), 652–654. https://doi.org/10/b4m7mh

Stokes, M. G. (2015). ‘Activity-silent’ working memory in prefrontal cortex: A dynamic coding framework. *Trends in Cognitive Sciences*, *19*(7), 394–405. https://doi.org/10.1016/j.tics.2015.05.004

Stokic, M., Milovanovic, D., Ljubisavljevic, M. R., Nenadovic, V., & Cukic, M. (2015). Memory load effect in auditory-verbal short-term memory task: EEG fractal and spectral analysis. *Experimental Brain Research*, *233*(10), 3023–3038. https://doi.org/10.1007/s00221-015-4372-z

Sutterer, D. W., Foster, J. J., Adam, K. C. S., Vogel, E. K., & Awh, E. (2019). Item-specific delay activity demonstrates concurrent storage of multiple active neural representations in working memory. *PLOS Biology*, *17*(4), e3000239. https://doi.org/10.1371/journal.pbio.3000239

Tallon-Baudry, C., Bertrand, O., Peronnet, F., & Pernier, J. (1998). Induced γ-Band Activity during the Delay of a Visual Short-Term Memory Task in Humans. *The Journal of Neuroscience*, *18*(11), 4244–4254.

Tallon-Baudry, C., Kreiter, A., & Bertrand, O. (1999). Sustained and transient oscillatory responses in the gamma and beta bands in a visual short-term memory task in humans. *Visual Neuroscience*, *16*(3), 449–459.

Teasdale, J. D., Proctor, L., Lloyd, C. A., & Baddeley, A. D. (1993). Working memory and stimulus-independent thought: Effects of memory load and presentation rate. *European Journal of Cognitive Psychology*, *5*(4), 417–433. https://doi.org/10.1080/09541449308520128

Tecce, J. J., Cattanach, L., Yrchik, D. A., Meinbresse, D., & Dessonville, C. L. (1982). CNV rebound and aging. *Electroencephalography and Clinical Neurophysiology*, *54*(2), 175–186. https://doi.org/10.1016/0013-4694(82)90159-6

Tecce, J. J., Savignano-Bowman, J., & Meinbresse, D. (1976). Contingent negative variation and the distraction—Arousal hypothesis. *Electroencephalography and Clinical Neurophysiology*, *41*(3), 277–286. https://doi.org/10.1016/0013-4694(76)90120-6

Tsubomi, H., Fukuda, K., Watanabe, K., & Vogel, E. K. (2013). Neural limits to representing objects still within view. *The Journal of Neuroscience*, *33*(19), 8257–8263. https://doi.org/10.1523/jneurosci.5348-12.2013

Unsworth, N., & Spillers, G. J. (2010). Working memory capacity: Attention control, secondary memory, or both? A direct test of the dual-component model. *Journal of Memory and Language*, *62*(4), 392–406. https://doi.org/10.1016/j.jml.2010.02.001

van Dijk, H., Schoffelen, J.-M., Oostenveld, R., & Jensen, O. (2008). Prestimulus Oscillatory Activity in the Alpha Band Predicts Visual Discrimination Ability. *Journal of Neuroscience*, *28*(8), 1816–1823. https://doi.org/10.1523/JNEUROSCI.1853-07.2008

van Driel, J., Gunseli, E., Meeter, M., & Olivers, C. N. L. (2017). Local and interregional alpha EEG dynamics dissociate between memory for search and memory for recognition. *NeuroImage*, *149*, 114–128. https://doi.org/10.1016/j.neuroimage.2017.01.031

van Ede, F. (2018). Mnemonic and attentional roles for states of attenuated alpha oscillations in perceptual working memory: A review. *The European Journal of Neuroscience*, *48*(7), 2509–2515. https://doi.org/10.1111/ejn.13759 van Ede, F., de Lange, F., Jensen, O., & Maris, E. (2011). Orienting Attention to an Upcoming Tactile Event Involves a Spatially and Temporally Specific Modulation of Sensorimotor Alpha- and Beta-Band Oscillations. *Journal of Neuroscience*, *31*(6), 2016–2024. https://doi.org/10.1523/JNEUROSCI.5630-10.2011

van Gerven, M., Bahramisharif, A., Heskes, T., & Jensen, O. (2009). Selecting features for BCI control based on a covert spatial attention paradigm. *Neural Networks*, *22*(9), 1271–1277. https://doi.org/10.1016/j.neunet.2009.06.004

Verleger, R. (1997). On the utility of P3 latency as an index of mental chronometry. *Psychophysiology*, *34*(2), 131–156. https://doi.org/10.1111/j.1469-8986.1997.tb02125.x

Violante, I. R., Li, L. M., Carmichael, D. W., Lorenz, R., Leech, R., Hampshire, A., … Sharp, D. J. (2017). Externally induced frontoparietal synchronization modulates network dynamics and enhances working memory performance. *ELife*, *6*. https://doi.org/10.7554/eLife.22001

Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature*, *428*(6984), 748–751. https://doi.org/10.1038/nature02447

Vogel, E. K., McCollough, A. W., & Machizawa, M. G. (2005). Neural measures reveal individual differences in controlling access to working memory. *Nature*, *438*(7067), 500.

Vogel, E. K., Woodman, G. F., & Luck, S. J. (2006). The time course of consolidation in visual working memory. *Journal of Experimental Psychology: Human Perception and Performance*, *32*(6), 1436–1451. https://doi.org/10.1037/0096-1523.32.6.1436

Vosskuhl, J., Huster, R. J., & Herrmann, C. S. (2015). Increase in short-term memory capacity induced by down-regulating individual theta frequency via transcranial alternating current stimulation. *Frontiers in Human Neuroscience*, *9*. https://doi.org/10.3389/fnhum.2015.00257

Wager, T. D., & Smith, E. E. (2003). Neuroimaging studies of working memory. *Cognitive, Affective, & Behavioral Neuroscience*, *3*(4), 255–274.

Walter, W. G., Cooper, R., Aldridge, V. J., McCallum, W. C., & Winter, A. L. (1964). Contingent Negative Variation: An Electric Sign of Sensori-Motor Association and Expectancy in the Human Brain. *Nature*, *203*(4943), 380–384. https://doi.org/10.1038/203380a0

Wang, H., Duan, J., Liao, Y., Wang, C., Li, H., & Liu, X. (2017). Objects Mental Rotation under 7 Days Simulated Weightlessness Condition: An ERP Study. *Frontiers in Human Neuroscience*, *11*. https://doi.org/10.3389/fnhum.2017.00553

Watter, S., Geffen, G. M., & Geffen, L. B. (2001). The n-back as a dual-task: P300 morphology under divided attention. *Psychophysiology*, *38*(6), 998–1003.

Weiss, S., & Mueller, H. M. (2012). "Too Many betas do not Spoil the Broth": The Role of Beta Brain Oscillations in Language Processing. *Frontiers in Psychology*, *3*. https://doi.org/10.3389/fpsyg.2012.00201

West, R., Bowry, R., & Krompinger, J. (2006). The effects of working memory demands on the neural correlates of prospective memory. *Neuropsychologia*, *44*(2), 197–207. https://doi.org/10.1016/j.neuropsychologia.2005.05.003

White, T. P., Jansen, M., Doege, K., Mullinger, K. J., Park, S. B., Liddle, E. B., … Liddle, Peter. F. (2013). Theta power during encoding predicts subsequent-memory performance and default mode network deactivation. *Human Brain Mapping*, *34*(11), 2929–2943. https://doi.org/10.1002/hbm.22114

Whittingstall, K., & Logothetis, N. K. (2009). Frequency-Band Coupling in Surface EEG Reflects Spiking Activity in Monkey Visual Cortex. *Neuron*, *64*(2), 281–289. https://doi.org/10.1016/j.neuron.2009.08.016

Wianda, E., & Ross, B. (2019). The roles of alpha oscillation in working memory retention. *Brain and Behavior*, e01263. https://doi.org/10.1002/brb3.1263

Wiegand, I., Hennig-Fast, K., Kilian, B., Müller, H. J., Töllner, T., Möller, H.-J., … Finke, K. (2016). EEG correlates of visual short-term memory as neuro-cognitive endophenotypes of ADHD. *Neuropsychologia*, *85*, 91–99. https://doi.org/10.1016/j.neuropsychologia.2016.03.011

Wiegand, I., Tollner, T., Habekost, T., Dyrholm, M., Muller, H. J., & Finke, K. (2014). Distinct neural markers of TVA-based visual processing speed and short-term storage capacity parameters. *Cerebral Cortex*, *24*(8), 1967–1978. https://doi.org/10.1093/cercor/bht071

Wiesman, A. I., Heinrichs-Graham, E., McDermott, T. J., Santamaria, P. M., Gendelman, H. E., & Wilson, T. W. (2016). Quiet connections: Reduced fronto-temporal connectivity in nondemented Parkinson's Disease during working memory encoding. *Human Brain Mapping*, *37*(9), 3224–3235. https://doi.org/10.1002/hbm.23237

Wijers, A. A., Otten, L. J., Feenstra, S., Mulder, G., & Mulder, L. J. (1989). Brain potentials during selective attention, memory search, and mental rotation. *Psychophysiology*, *26*(4), 452–467. https://doi.org/10.1111/j.1469-8986.1989.tb01951.x

Wilson, G. F., Swain, C. R., & Ullsperger, P. (1999). EEG power changes during a multiple level memory retention task. *International Journal of Psychophysiology*, *32*(2), 107–118. https://doi.org/10/dkvzj9

Wilson, T. W., Proskovec, A. L., Heinrichs-Graham, E., O'Neill, J., Robertson, K. R., Fox, H. S., & Swindells, S. (2017). Aberrant Neuronal Dynamics during Working Memory Operations in the Aging HIV-Infected Brain. *Scientific Reports*, *7*, 41568. https://doi.org/10.1038/srep41568

Winkler, I., Debener, S., Muller, K.-R., & Tangermann, M. (2015). On the influence of high-pass filtering on ICA-based artifact reduction in EEG-ERP. *2015 37th Annual International Conference of the IEEE Engineering in Medicine and Biology Society (EMBC)*, 4101–4105. https://doi.org/10.1109/EMBC.2015.7319296

Wisniewski, M. G., Iyer, N., Thompson, E. R., & Simpson, B. D. (2018). Sustained frontal midline theta enhancements during effortful listening track working memory demands. *Hearing Research*, *358*, 37–41. https://doi.org/10.1016/j.heares.2017.11.009

Wisniewski, M. G., Thompson, E. R., & Iyer, N. (2017). Theta- and alpha-power enhancements in the electroencephalogram as an auditory delayed match-to-sample task becomes impossibly difficult. *Psychophysiology*, *54*(12), 1916–1928. https://doi.org/10.1111/psyp.12968

Wolach, I., & Pratt, H. (2001). The mode of short-term memory encoding as indicated by event-related potentials in a memory scanning task with distractions. *Clinical Neurophysiology*, *112*(1), 186–197. https://doi.org/10.1016/S1388-2457(00)00501-0

Wolff, M. J., Ding, J., Myers, N. E., & Stokes, M. G. (2015). Revealing hidden states in visual working memory using electroencephalography. *Frontiers in Systems Neuroscience*, *9*, 123. https://doi.org/10.3389/fnsys.2015.00123

Wolff, M. J., Jochim, J., Akyürek, E. G., & Stokes, M. G. (2017). Dynamic hidden states underlying working-memory-guided behavior. *Nature Neuroscience*, *20*(6), 864. https://doi.org/10.1038/nn.4546

Wolff, M. J., Kandemir, G., Stokes, M. G., & Akyürek, E. G. (2019). Impulse responses reveal unimodal and bimodal access to visual and auditory working memory. *BioRxiv*. https://doi.org/10.1101/623835

Wolinski, N., Cooper, N. R., Sauseng, P., & Romei, V. (2018). The speed of parietal theta frequency drives visuospatial working memory capacity. *PLOS Biology*, *16*(3), e2005348. https://doi.org/10.1371/journal.pbio.2005348

Worden, M. S., Foxe, J. J., Wang, N., & Simpson, G. V. (2000). Anticipatory biasing of visuospatial attention indexed by retinotopically specific-band electroencephalography increases over occipital cortex. *Journal of Neuroscience*, *20*(RC63), 1–6.

Xie, Y., Feng, Z., Xu, Y., Bian, C., & Li, M. (2016). The different oscillation patterns of alpha band in the early and later stages of working memory maintenance. *Neuroscience Letters*, *633*, 220–226. https://doi.org/10.1016/j.neulet.2016.09.047

Xing, Y., Ledgeway, T., McGraw, P. V., & Schluppeck, D. (2013). Decoding Working Memory of Stimulus Contrast in Early Visual Cortex. *Journal of Neuroscience*, *33*(25), 10301–10311. https://doi.org/10.1523/JNEUROSCI.3754-12.2013

Yin, J., Gao, Z., Jin, X., Ding, X., Liang, J., & Shen, M. (2012). The neural mechanisms of percept-memory comparison in visual working memory. *Biological Psychology*, *90*(1), 71–79. https://doi.org/10.1016/j.biopsycho.2012.02.023

Yu, X., Chen, Y., Qiu, J., Li, X., & Huang, X. (2017). Neural oscillations associated with auditory duration maintenance in working memory. *Scientific Reports*, *7*(1), 5695. https://doi.org/10.1038/s41598-017-06078-2

Zakrzewska, M. Z., & Brzezicka, A. (2014). Working memory capacity as a moderator of load-related frontal midline theta variability in Sternberg task. *Frontiers in Human Neuroscience*, *8*, 399. https://doi.org/10.3389/fnhum.2014.00399

Zhang, D., Zhao, H., Bai, W., & Tian, X. (2016). Functional connectivity among multi-channel EEGs when working memory load reaches the capacity. *Brain Research*, *1631*, 101–112. https://doi.org/10.1016/j.brainres.2015.11.036

Appendix

Table A1 – EEG studies that investigated neural oscillations during WM delay

Reference	**N**	**Delay, s**	**Modality**	**Load**	**Components**	**Ind. diff.**
Wisniewski et al., 2018	10	3	auditory			
Wisniewski, Thompson, & Iyer, 2017	14	2,5	auditory	+		
Yu et al., 2017	25	3	auditory			
Backer, Binns, & Alain, 2015	16	1,1-2	auditory-spatial			
Bastiaansen et al., 2002	174	1 or 4	spatial			
Herding, Spitzer, & Blankenburg, 2016	18	1	tactile			
Spitzer & Blankenburg, 2011	25	2,5	tactile			
Spitzer et al., 2014	24	2,5	tactile			
Spitzer, Wacker, & Blankenburg, 2010	14	1,75	tactile			
Al-Qazzaz et al., 2015	10	60 (1 trial)	verbal			
Bashivan et al., 2014	15	3	verbal	+		
Berger et al., 2014	19	2	verbal		+	
Chou et al., 2015	64	0,6	verbal			
Gao et al., 2018	26	3	verbal	+		
Griesmayr et al., 2010	15	2,5	verbal		+	
Harmony et al., 1996	10	2	verbal	+		
Itthipuripat, Wessel, & Aron, 2013	13	1,5	verbal		+	
Jensen et al., 2002	10	2,8	verbal	+		
Klimesch et al., 1993	16	2	verbal	+		
Klimesch et al., 1999	14	8	verbal	+		
Kottlow et al., 2015	22	3,5	verbal	+		
Kwon et al., 2015	17	5	verbal	+		+
Meltzer et al., 2007	18	10,85	verbal	+		
Michels et al., 2008	18	3	verbal	+		
Michels et al., 2010	16	3,5	verbal	+		
Okuhata, Kusanagi, & Kobayashi, 2013	10	3,2	verbal	+		

Onton, Delorme, & Makeig, 2005	23	2-4	verbal	+		
Park, Min, et al., 2013	22	1,5	verbal	+		
Pavlov & Kotchoubey, 2017	56	6,7	verbal	+	+	+
Schack & Klimesch, 2002	10	1,8	verbal	+		
Scheeringa et al., 2009	20	7	verbal	+		
Wilson, Swain, & Ullsperger, 1999	10	4	verbal	+		
Xie et al., 2016	16	2	verbal	+		
Zakrzewska & Brzezicka, 2014	69	2,5	verbal	+		+
Fingelkurts et al., 2002	9	2	verbal (auditory)			
Kawasaki, Kitajo, & Yamaguchi, 2010	14	2	verbal (auditory)		+	
Melnik, Mapelli, & Ozkurt, 2017	25	2,5	verbal (auditory)			
Stokic et al., 2015	20	5	verbal (auditory)	+		
Hwang et al., 2005	12	0,5	verbal, visual			
Khader et al., 2010	17	5-7	verbal, visual			
Babiloni et al., 2004	12	3,5-5,5	visual			
Blacker et al., 2016	18	2	visual			
Boonstra et al., 2013	8	6	visual	+		
Busch & Herrmann, 2003	16	3	visual	+		
Crespo-Garcia et al., 2013	29	2,5-5	visual	+		
de Vries et al., 2018	20	1,4	visual			
Ellmore, Ng, & Reichert, 2017	15	6	visual			
Eschmann, Bader, & Mecklinger, 2018	27	2	visual		+	
Fukuda, Mance, & Vogel, 2015	33	1-4	visual	+		
Heinz & Johnson, 2017	18	1,4	visual	+		
Herrmann, Senkowski, & Rottger, 2004	22	3-4	visual			

Honkanen et al., 2015 (Exp. 1)	13	2,05	visual	+		
Honkanen et al., 2015 (Exp. 2)	8	2,05	visual	+		
Hsieh, Ekstrom, & Ranganath, 2011	21	4	visual			+
Huang et al., 2013	64	0,8	visual			
Ikkai et al., 2014	18	2	visual			
Johnson et al., 2011	12	3	visual			
Kawasaki & Watanabe, 2007	9	1	visual		+	
Kawasaki & Yamaguchi, 2012	19	2	visual	+		
Kawasaki & Yamaguchi, 2013	14	2	visual	+		+
Kawasaki, Kitajo, & Yamaguchi, 2010	14	2	visual		+	
Manza, Hau, & Leung, 2014	31	2	visual	+		
Mapelli & Ozkurt, 2019	28	1-1,5	visual			
Maurer et al., 2015	24	3,5	visual	+		
Myers et al., 2015	18	0,8	visual			
Nenert et al., 2012	16	1-3	visual	+		
Pahor & Jausovec, 2017	60	1	visual	+		+
Palva et al., 2010	13	1	visual	+		
Park, Min, & Lee, 2010	10	0,5	visual			
Poch et al., 2018	36	1	visual	+		
Rawle, Miall, & Praamstra, 2012	20	1,1	visual	+		
Roberts, Hsieh, & Ranganath, 2013	16	4	visual			
Sauseng et al., 2005	23	2.5	visual		+	
Sauseng et al., 2009	16	0,9	visual	+		
Schneider, Barth, & Wascher, 2017	18	0,5	visual			
Schneider, Mertes, & Wascher, 2015	12	0,5	visual			
Smyrnis et al., 2014	10	3,5-4,5	visual			
Tallon-Baudry et al., 1998	13	0,8	visual			
Tallon-Baudry, Kreiter, & Bertrand, 1999	13	0,8-1,6	visual			

van Driel et al., 2017	20	0,9	visual			
Vries, Driel, & Olivers, 2017	20	1,8	visual	+		
Yin et al., 2012	12	1	visual			
Zhang et al., 2016	16	3	visual	+		
Seemuller, Muller, & Rosler, 2012	17	1	visual, kinestetic			
Spitzer & Blankenburg, 2012	28	3	visual, tactile, auditory			
Spitzer, Fleck, & Blankenburg, 2014	24	3	visual, tactile, auditory	+		

Table A2 – verbal WM load effects in EEG

Reference	**Theta**	**Alpha**	**Beta**	**Gamma**
Al-Qazzaz et al., 2015	-	-	-	-
Bashivan et al., 2014	-	+See text	0	-
Berger et al., 2014	+↑	+↑	+↓	-
Chou et al., 2015	+↑	+↑	+↑	-
Fingelkurts et al., 2002	+↑	+See text	-	-
Gao et al., 2018	+↑	-	0	0
Griesmayr et al., 2010	+↑	-	-	-
Harmony et al., 1996	+↑	+↓	-	-
Hwang et al., 2005	-	+↓	+↓	+↓
Itthipuripat, Wessel, & Aron, 2013	+↑	+↑	+↓	0
Jensen et al., 2002	+↟	+↑	-	-
Kawasaki, Kitajo, & Yamaguchi, 2010	+↑	+↑	-	-
Khader et al., 2010	+↑	+↑	-	-
Klimesch et al., 1999	+↟	+↑	-	-
Klimesch, Schimke, & Pfurtscheller, 1993	-	+↑	-	-
Kottlow et al., 2015	+↟	+See text	+See text	-
Kwon et al., 2015	+↑	+↓	-	-
Melnik, Mapelli, & Ozkurt, 2017	-	+↑	-	-
Meltzer et al., 2007	+↟	+↓	-	-
Michels et al., 2008	+↟	+See text	-	-
Michels et al., 2010	+↟	+↑	+↓	0
Okuhata, Kusanagi, & Kobayashi, 2013	-	+See text	-	-
Onton, Delorme, & Makeig, 2005	+↟	-	+↑	-
Park, Min, et al., 2013	+↟	-	0	-

Pavlov & Kotchoubey, 2017	+ See text	+See text	+See text	-
Schack & Klimesch, 2002	+↑	+↑	-	-
Scheeringa et al., 2009	+↟	+↑	-	-
Stokic et al., 2015	+↟	+↓	+↑	-
Wilson, Swain, & Ullsperger, 1999	+↟	+↓	+↓	-
Xie, Feng, Xu, Bian, & Li, 2016	-	+See text	-	-
Zakrzewska & Brzezicka, 2014	+↟	-	-	-

Notes: + – featured in the results of the paper, - – not featured in the results, ↟ - step-wise increase of activity, 0 - no changes, ↑ - increase, ↓ - decrease, see text – complex results described in main text of the systematic review

References to Tables A1 and A2: (Al-Qazzaz, Bin Mohd Ali, Ahmad, Islam, & Escudero, 2015; Babiloni et al., 2004; Backer, Binns, & Alain, 2015; Bashivan et al., 2014; Bastiaansen et al., 2002; Berger et al., 2014; Blacker, Ikkai, Lakshmanan, Ewen, & Courtney, 2016; Boonstra et al., 2013; Busch & Herrmann, 2003; Chou, Duann, She, Huang, & Jung, 2015; Crespo-Garcia et al., 2013; de Vries et al., 2017, 2018; Ellmore et al., 2017; Eschmann et al., 2018; Fingelkurts, Fingelkurts, Krause, & Sams, 2002; Fukuda et al., 2015; Gao, Sun, Yang, & Gong, 2018; Griesmayr et al., 2010; Harmony et al., 1996; Heinz & Johnson, 2017; Herding, Spitzer, & Blankenburg, 2016; Herrmann, Senkowski, & Rottger, 2004; Honkanen, Rouhinen, Wang, Palva, & Palva, 2015; Hsieh et al., 2011; Huang et al., 2013; Hwang et al., 2005; Ikkai et al., 2014; Itthipuripat et al., 2013; Jensen, Gelfand, Kounios, & Lisman, 2002; Johnson et al., 2011; Kawasaki et al., 2010; Kawasaki & Watanabe, 2007; Kawasaki & Yamaguchi, 2012, 2013; Khader et al., 2010; Klimesch et al., 1999, 1993; Kottlow et al., 2015; Kwon et al., 2015; Manza, Hau, & Leung, 2014; Mapelli & Ozkurt, 2019; Maurer et al., 2015; Melnik, Mapelli, & Ozkurt, 2017; Meltzer et al., 2007; Michels et al., 2010, 2008; Myers et al., 2015; Nenert, Viswanathan, Dubuc, & Visscher, 2012; Okuhata et al., 2013; Onton et al., 2005; Pahor & Jausovec, 2017; Palva et al., 2010; Park, Min, & Lee, 2010; Park, Jhung, Lee, & An, 2013; Pavlov & Kotchoubey, 2017; Poch, Valdivia, Capilla, Hinojosa, & Campo, 2018; Rawle, Miall, & Praamstra, 2012; Roberts et al., 2013; Sauseng, Klimesch, Doppelmayr, et al., 2005; Schack & Klimesch, 2002; Scheeringa et al., 2009; Schneider, Barth, & Wascher, 2017; Schneider, Mertes, & Wascher, 2015; Seemuller, Muller, & Rosler, 2012; Smyrnis et al., 2014; Spitzer & Blankenburg, 2012; Spitzer, Fleck, & Blankenburg, 2014; Spitzer, Gloel, Schmidt, & Blankenburg, 2014; Spitzer et al., 2010; Stokic et al., 2015; Tallon-Baudry et al., 1998; Tallon-Baudry, Kreiter, & Bertrand, 1999; van Driel, Gunseli, Meeter, & Olivers, 2017; Wilson, Swain, & Ullsperger, 1999; Wisniewski, Iyer, Thompson, & Simpson, 2018; Wisniewski, Thompson, & Iyer, 2017; Xie et al., 2016; Yin et al., 2012; Yu, Chen, Qiu, Li, & Huang, 2017; Zakrzewska & Brzezicka, 2014; Zhang et al., 2016)

Table A3 – LME analysis’ of SCP statistical output

	β	*SE*	*t*	*p*
Amplitude ~ Task * Load * TimeInt * Channel * Performance + (1 + Task + Load + TimeInt + Channel | Participant)				
(Intercept)	-0.0002	0.0119	-0.02	0.985
Performance	-0.0032	0.0119	-0.27	0.790
Task:Performance	0.0010	0.0068	0.15	0.883
Load:Performance	-0.0101	0.0079	-1.27	0.206
TimeInt:Performance	-0.0180	0.0071	-2.52	0.013
Channel:Performance	0.0028	0.0079	0.36	0.722
Task:Load:Performance	-0.0042	0.0030	-1.39	0.165
Task:TimeInt:Performance	-0.0004	0.0030	-0.15	0.885
Load:TimeInt:Performance	-0.0029	0.0037	-0.78	0.439
Task:Channel:Performance	-0.0048	0.0030	-1.57	0.115
Load:Channel:Performance	0.0021	0.0037	0.55	0.580
TimeInt:Channel:Performance	-0.0040	0.0037	-1.08	0.280
Task:Load:TimeInt:Performance	0.0025	0.0037	0.67	0.503
Task:Load:Channel:Performance	0.0039	0.0037	1.06	0.289
Task:TimeInt:Channel:Performance	0.0015	0.0037	0.41	0.682
Load:TimeInt:Channel:Performance	-0.0004	0.0045	-0.09	0.925
Task:Load:TimeInt:Channel:Performance	0.0032	0.0045	0.71	0.478
Amplitude ~ Task * Load * TimeInt * AntPos * Hemisphere * Performance + (1 + Task + Load + TimeInt + Hemisphere + AntPos | Participant)				
(Intercept)	0.0002	0.0073	0.02	0.981
Performance	-0.0015	0.0073	-0.21	0.837
Task:Performance	-0.0002	0.0062	-0.04	0.969
Load:Performance	-0.0093	0.0062	-1.51	0.133
TimeInt:Performance	-0.0040	0.0060	-0.66	0.510
AntPos:Performance	0.0005	0.0043	0.11	0.911
Hemisphere:Performance	0.0065	0.0028	2.33	0.021
Task:Load:Performance	0.0035	0.0027	1.30	0.192
Task:TimeInt:Performance	-0.0010	0.0027	-0.38	0.704
Load:TimeInt:Performance	-0.0063	0.0033	-1.92	0.055
Task:AntPos:Performance	-0.0055	0.0022	-2.56	0.010
Load:AntPos:Performance	0.0062	0.0027	2.35	0.019
TimeInt:AntPos:Performance	0.0036	0.0026	1.35	0.178
Task:Hemisphere:Performance	-0.0006	0.0022	-0.28	0.777
Load:Hemisphere:Performance	0.0026	0.0027	0.99	0.325
TimeInt:Hemisphere:Performance	0.0006	0.0026	0.24	0.812
AntPos:Hemisphere:Performance	0.0002	0.0022	0.08	0.936
Task:Load:TimeInt:Performance	0.0047	0.0033	1.46	0.145
Task:Load:AntPos:Performance	-0.0021	0.0027	-0.78	0.438
Task:TimeInt:AntPos:Performance	-0.0014	0.0026	-0.54	0.592
Load:TimeInt:AntPos:Performance	0.0055	0.0033	1.69	0.091
Task:Load:Hemisphere:Performance	0.0001	0.0027	0.04	0.968

Task:TimeInt:Hemisphere:Performance	-0.0010	0.0026	-0.37	0.712
Load:TimeInt:Hemisphere:Performance	0.0002	0.0033	0.06	0.949
Task:AntPos:Hemisphere:Performance	0.0014	0.0022	0.64	0.525
Load:AntPos:Hemisphere:Performance	0.0015	0.0027	0.57	0.572
TimeInt:AntPos:Hemisphere:Performance	0.0011	0.0026	0.40	0.691
Task:Load:TimeInt:AntPos:Performance	0.0002	0.0033	0.06	0.956
Task:Load:TimeInt:Hemisphere:Performance	-0.0022	0.0033	-0.67	0.505
Task:Load:AntPos:Hemisphere:Performance	-0.0029	0.0027	-1.11	0.268
Task:TimeInt:AntPos:Hemisphere:Performance	0.0005	0.0026	0.20	0.842
Load:TimeInt:AntPos:Hemisphere:Performance	-0.0005	0.0033	-0.16	0.876
Task:Load:TimeInt:AntPos:Hemisphere: Performance	<0.0001	0.0033	<0.01	0.999